Collective Animal Behavior

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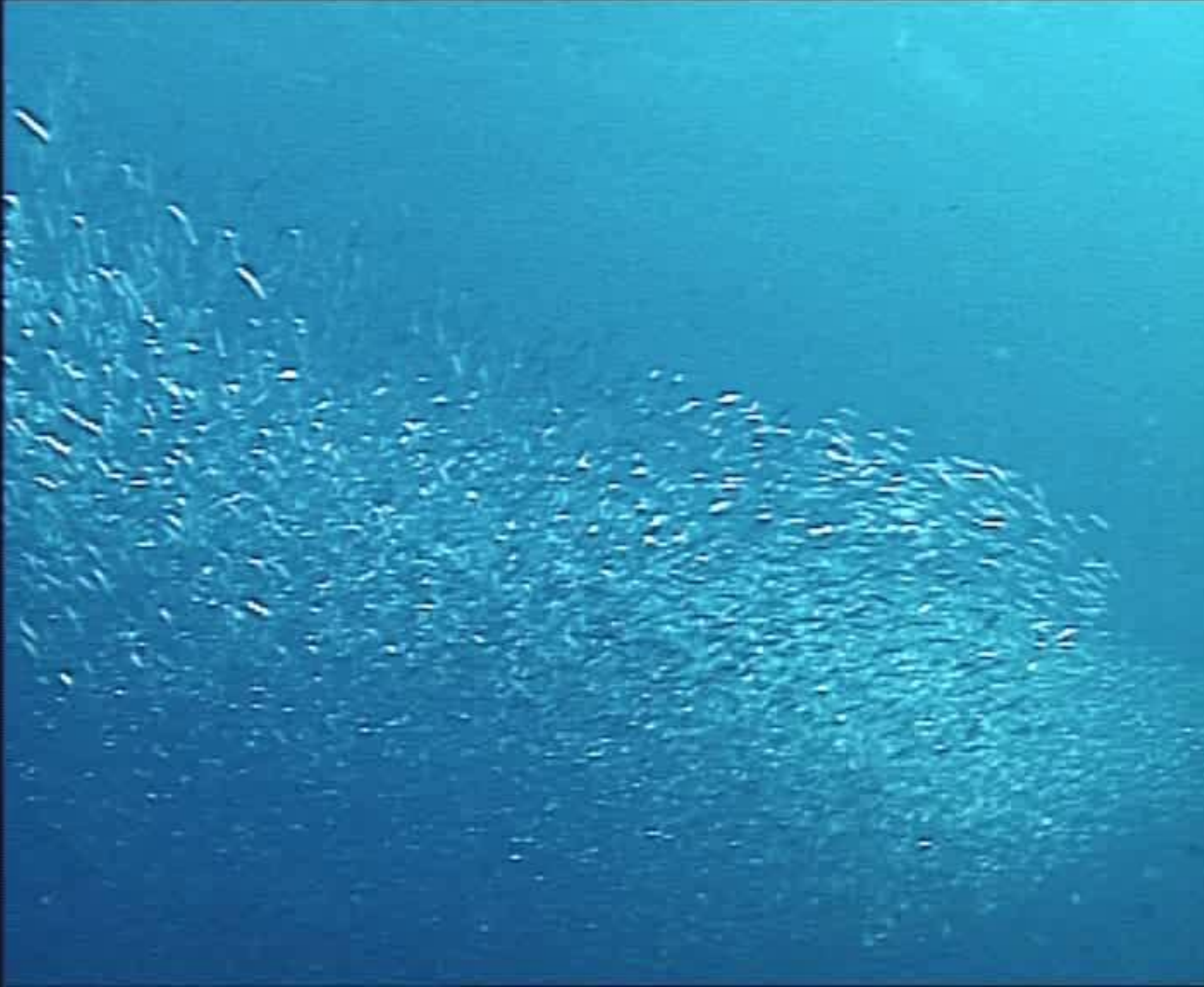
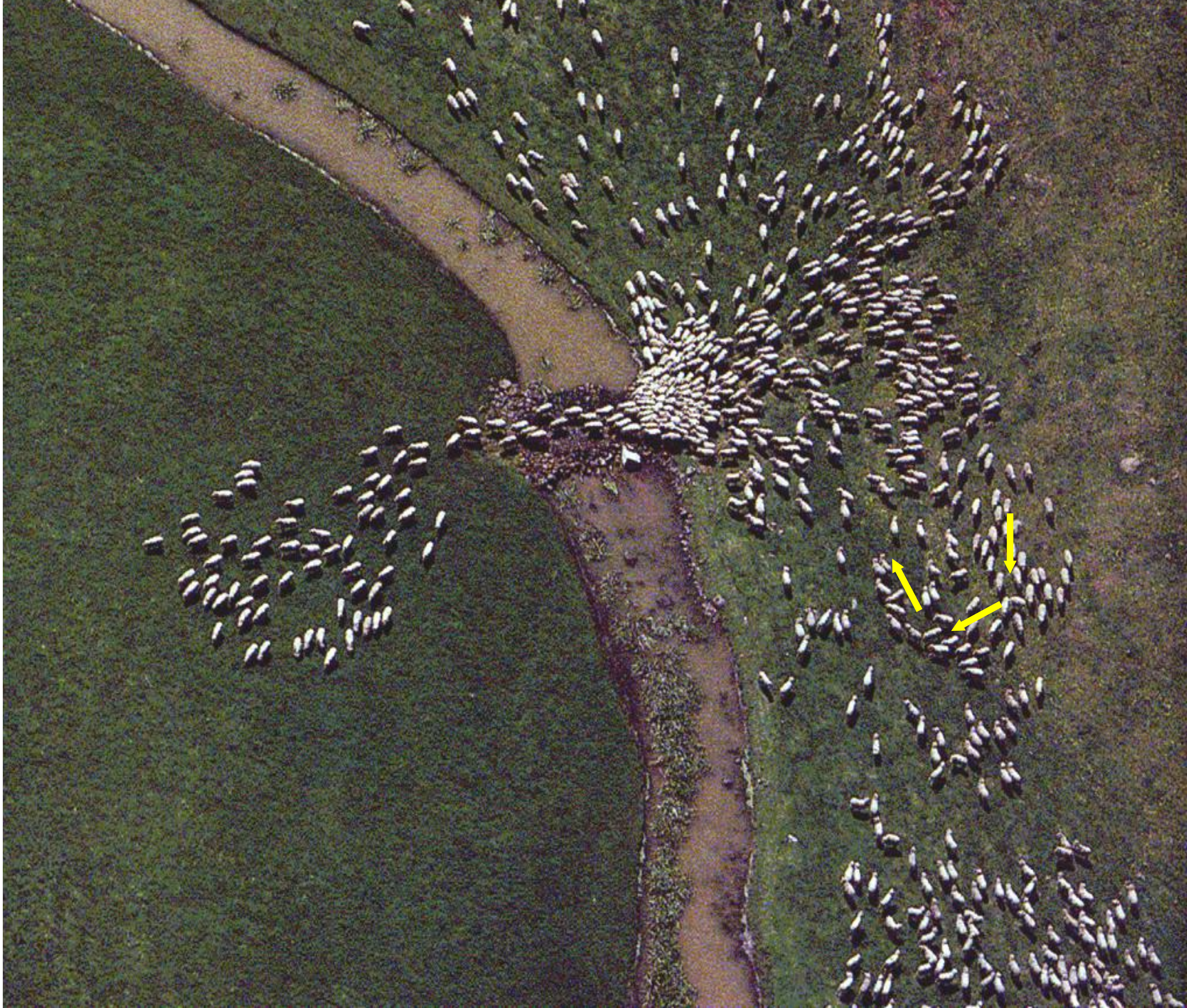
Program in Applied and Computational Mathematics

COLLECTIVE ANIMAL BEHAVIOUR

Princeton University



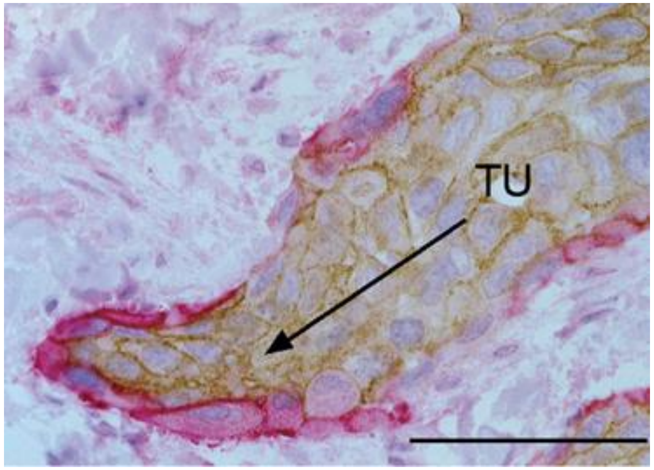
Introduction

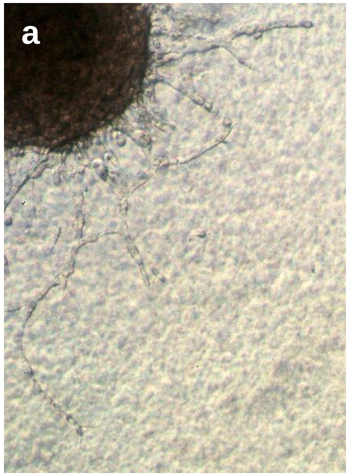


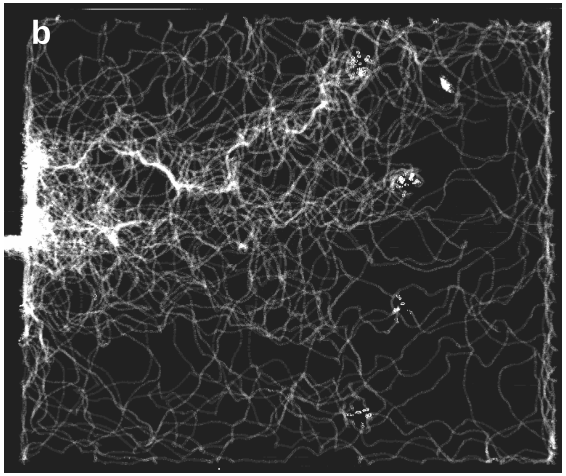
Introduction

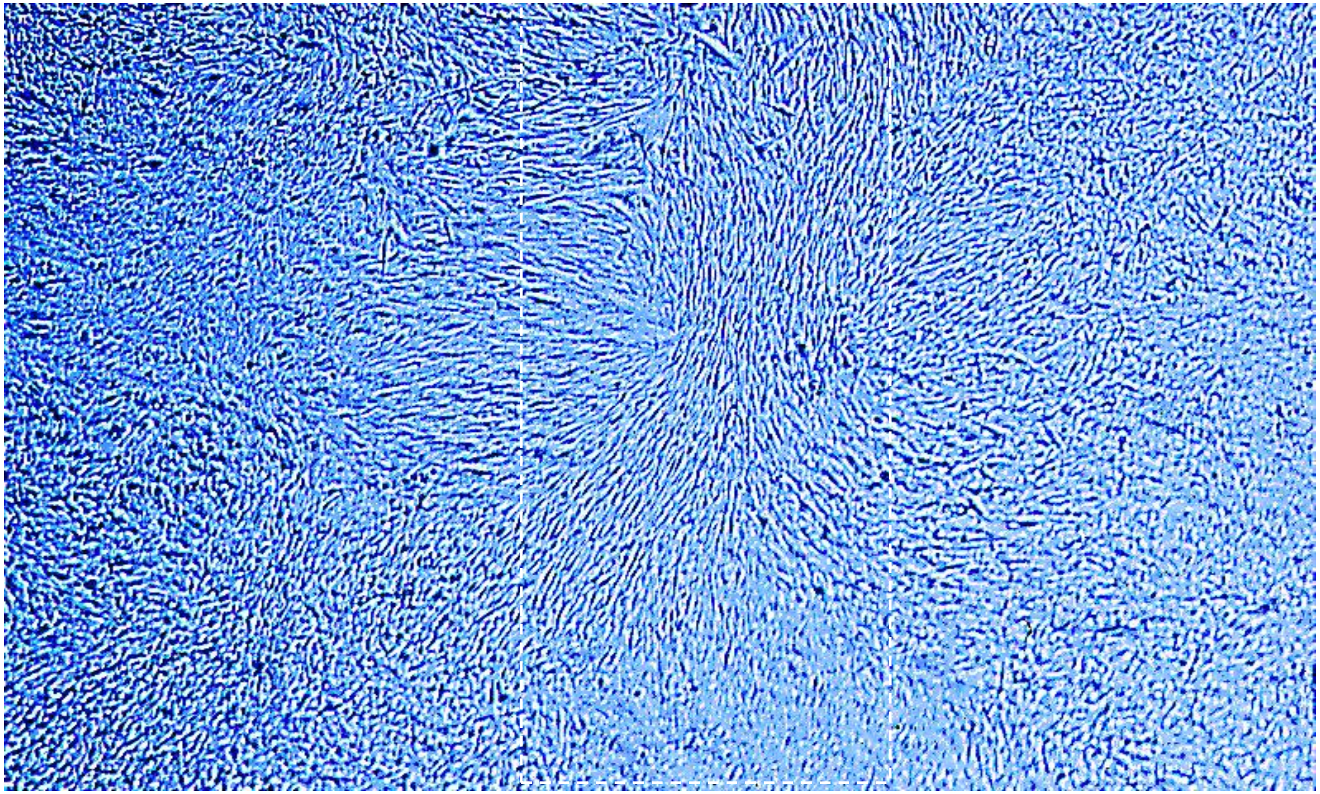
Why animal groups?

Introduction





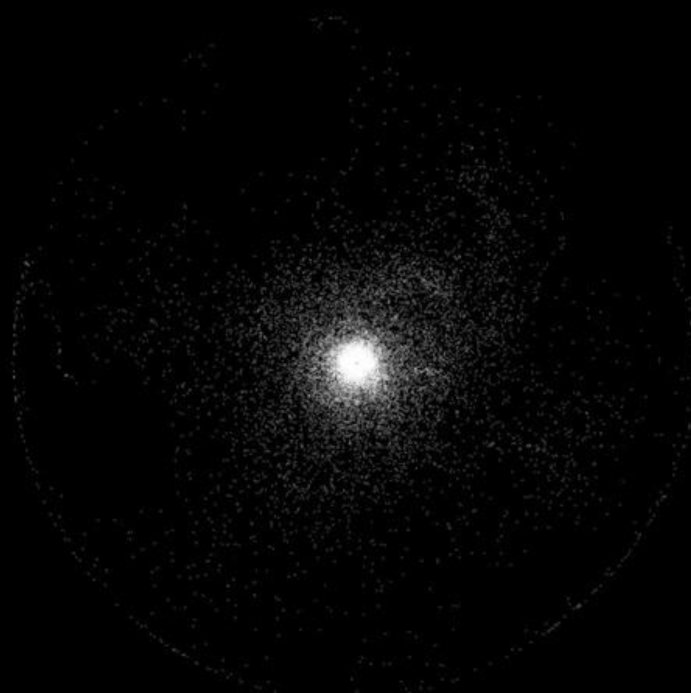




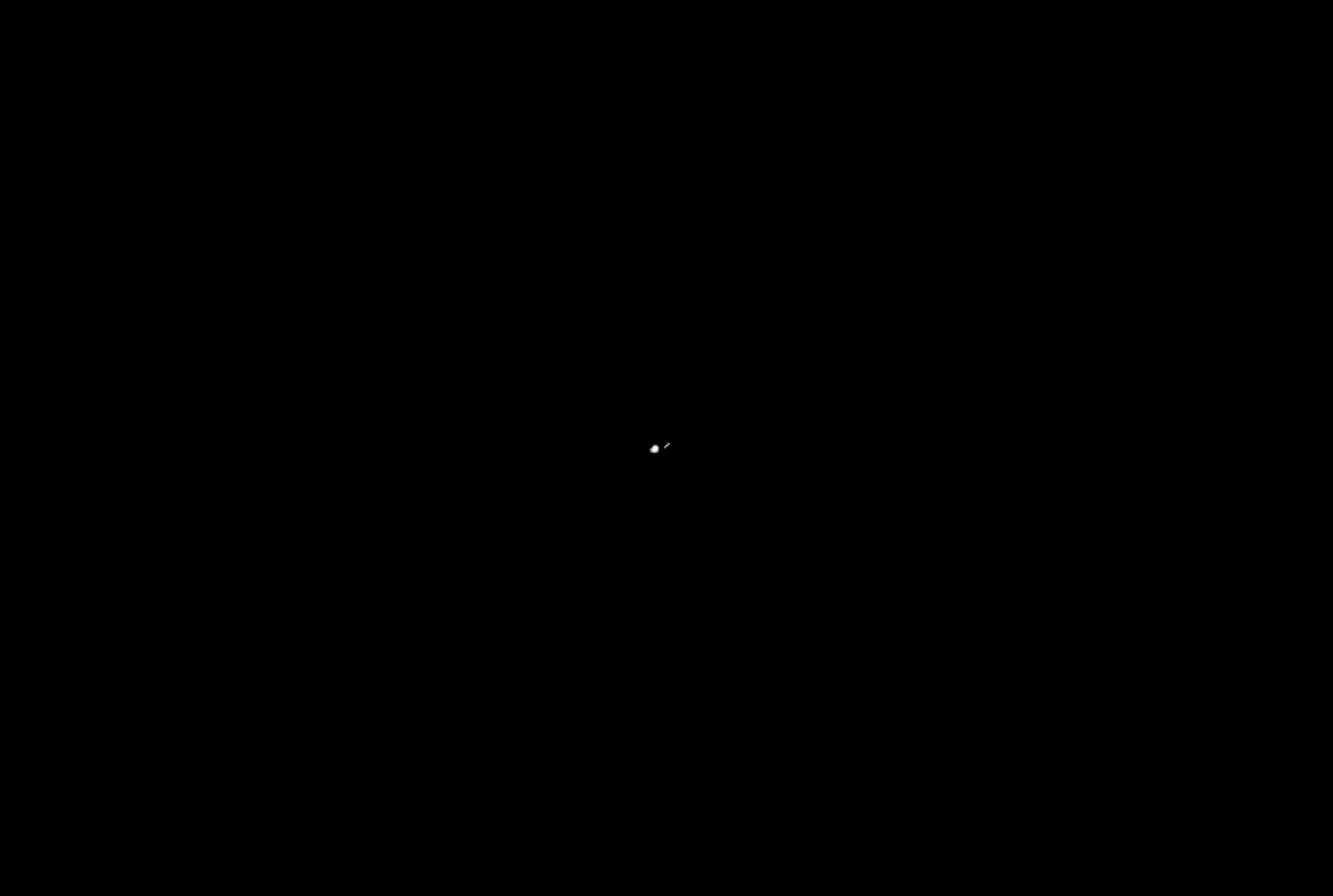
Deisboeck & Couzin (2009) Collective behavior in cancer cell populations. *BioEssays*

Introduction

Environmental Feedbacks, environmental modification

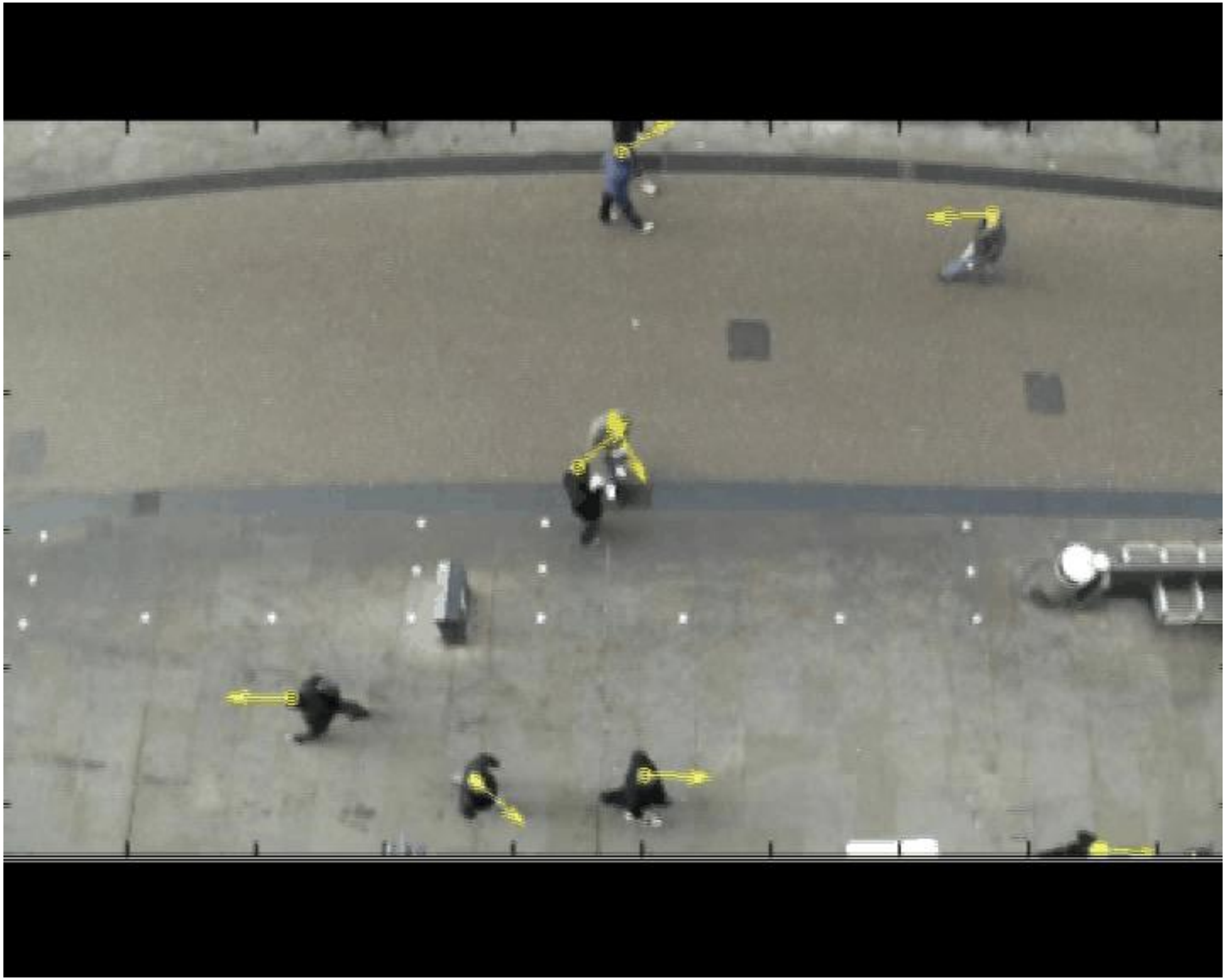


With Simon Garnier



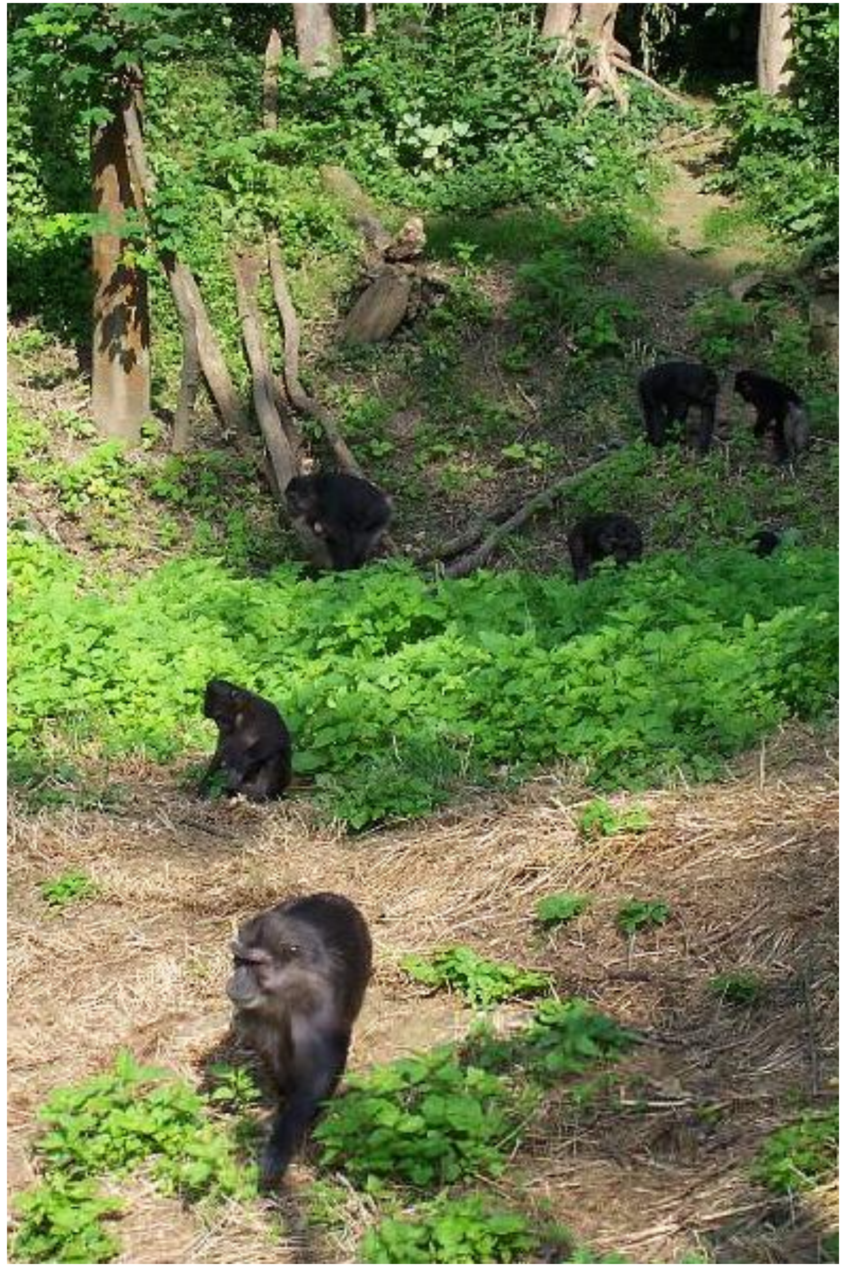
With Simon Garnier

With Simon Garnier, Simon Leblanc



with Joe Hale and Simon Garnier

Introduction

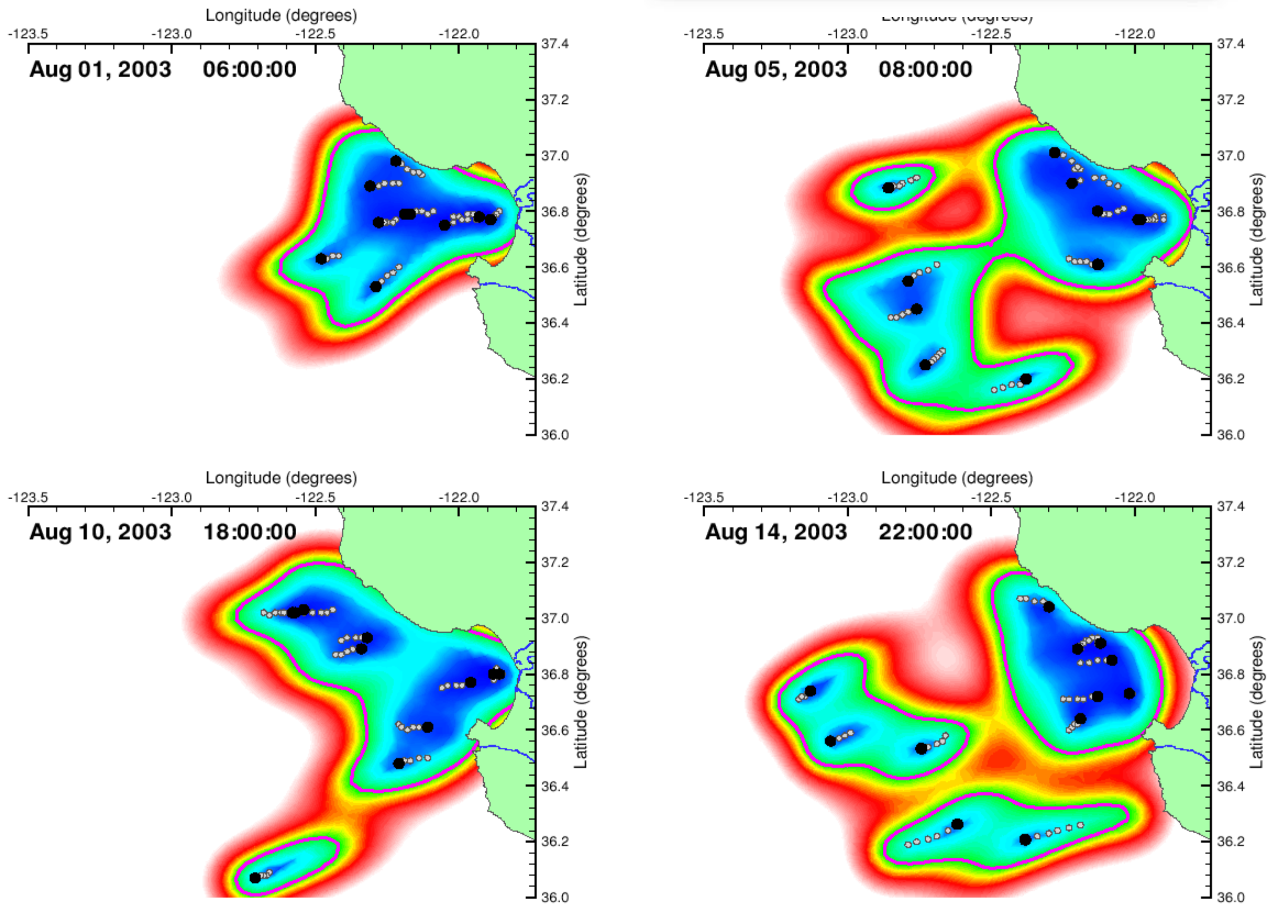


Cedric Sueur

Introduction

Naomi Leonard

Mechanical and Aerospace Engineering
Princeton University



Overview

Locust hopper bands

Group motion and collective memory

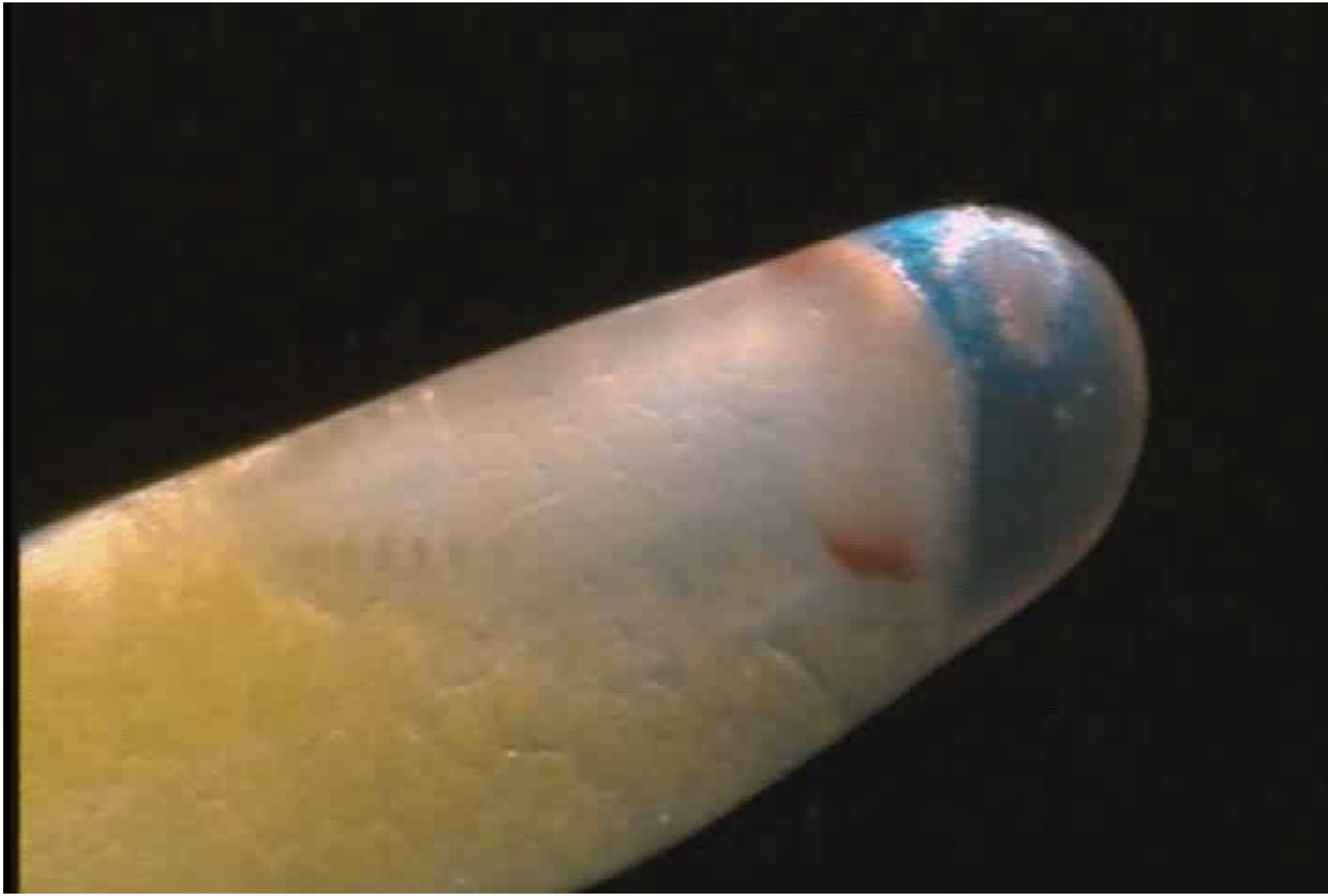
Collective decision-making

Evolution of collective behavior

Mass migration

Locust hopper bands

Locust hopper bands



Locust hopper bands

During plagues, the Desert Locust has the potential to damage the livelihood of one tenth of the world's population

Food and Agriculture Organization of the United Nations (FAO)

During plagues, the Desert Locust has the potential to damage the livelihood of one tenth of the world's population

Food and Agriculture Organization of the United Nations (FAO)

Understanding when and where marching bands will form is critical as they are easier to control and inevitably precede outbreaks of winged insects.

Locust hopper bands

During plagues, the Desert Locust has the potential to damage the livelihood of one tenth of the world's population

Food and Agriculture Organization of the United Nations (FAO)

Understanding when and where marching bands will form is critical as they are easier to control and inevitably precede outbreaks of winged insects.

“Even after 50 years of experience, fighting locusts is more of an art than a science”

Enserink (2004) *Science*.

With Jerome Buhl, David Sumpter

Science (2006) **312**, 1402-1406

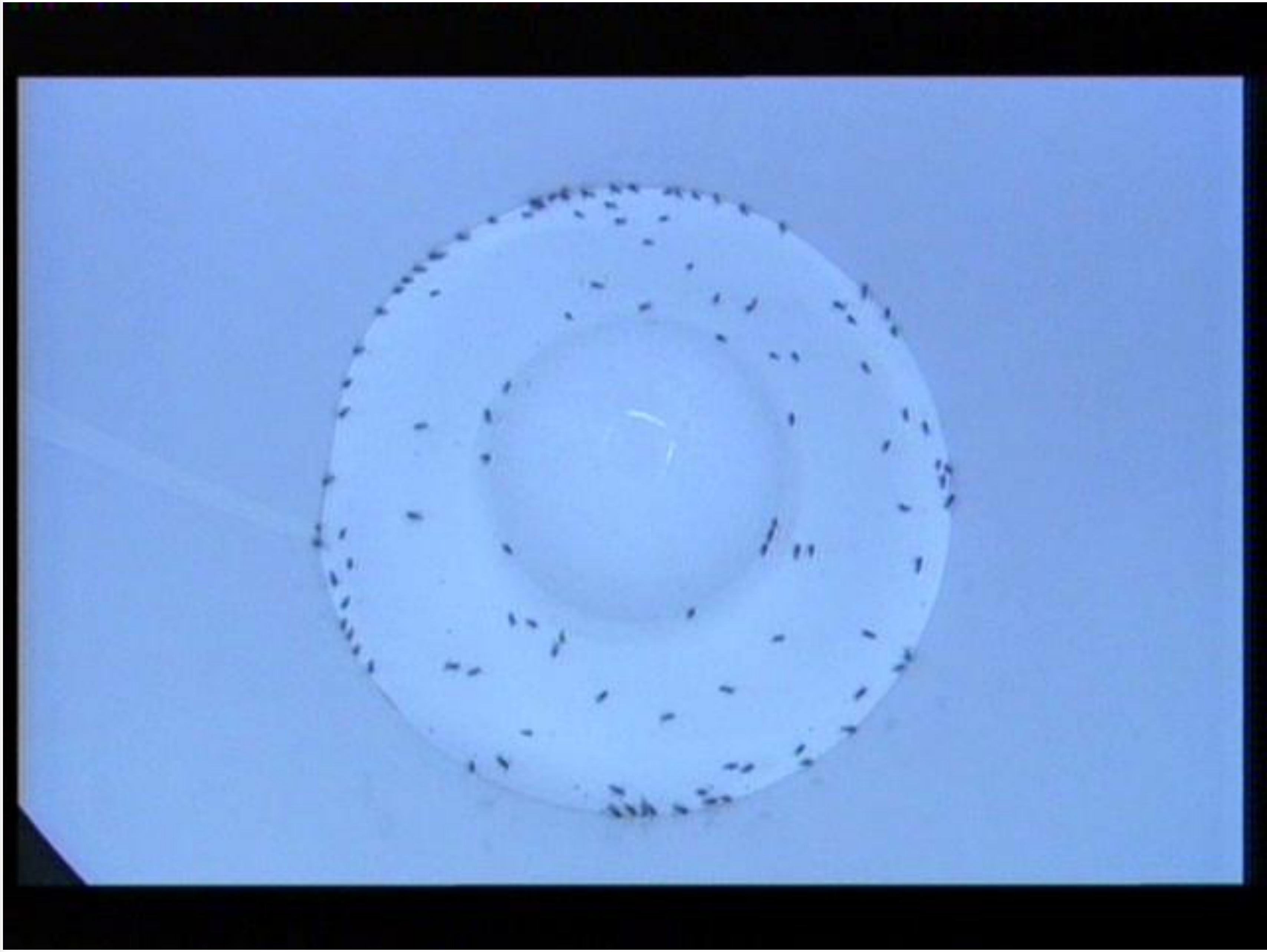
From disorder to order in marching locusts

What is the relationship between insect density and collective motion in locusts?

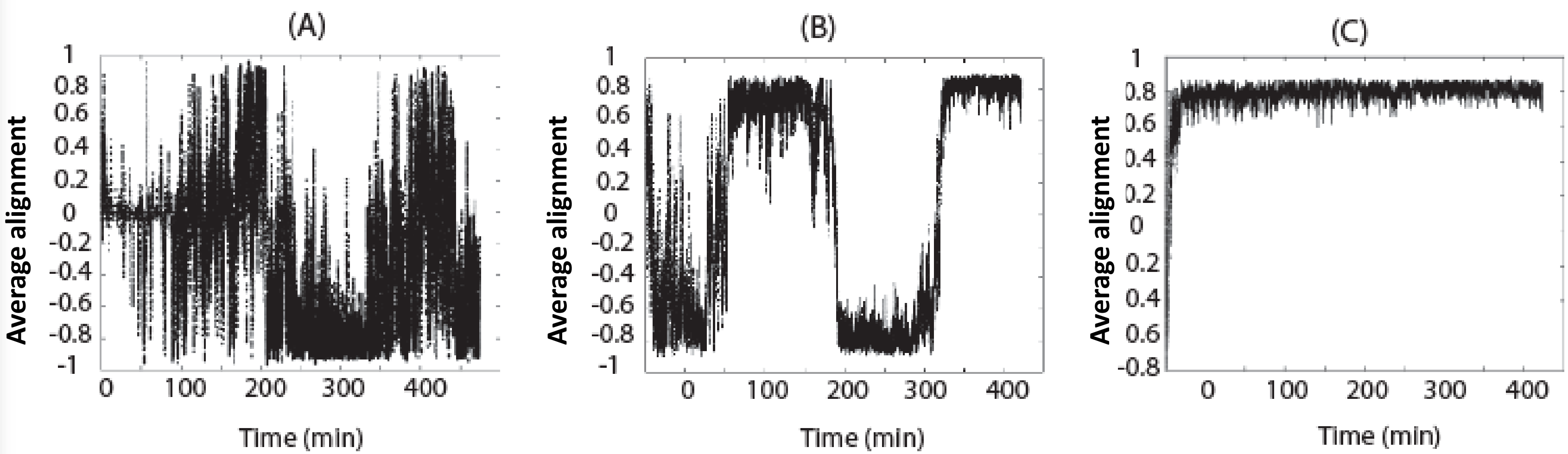
Locust hopper bands

With Jerome Buhl, David Sumpter

Science (2006) **312**, 1402-1406



Locust hopper bands



Increasing density

Locust hopper bands

Non-magnetic

Magnetic

Increase heat

(770ºC)

Minimal ingredients– insights from non-linear statistical physics

constant self-propulsion = 0.1

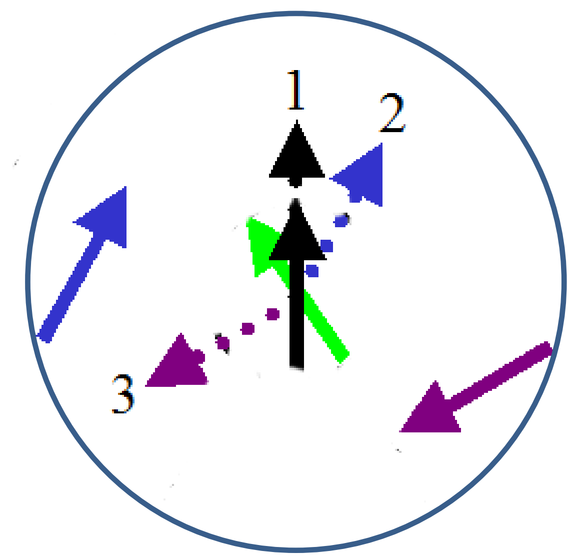
position

$$\boxed{x_i}(t+1) = x_i(t) + v_0 \boxed{u_i}(t),$$

$$\boxed{u_i}(t+1) = G\Big(\langle u(t)\rangle_i\Big) + \boxed{\xi_i}.$$

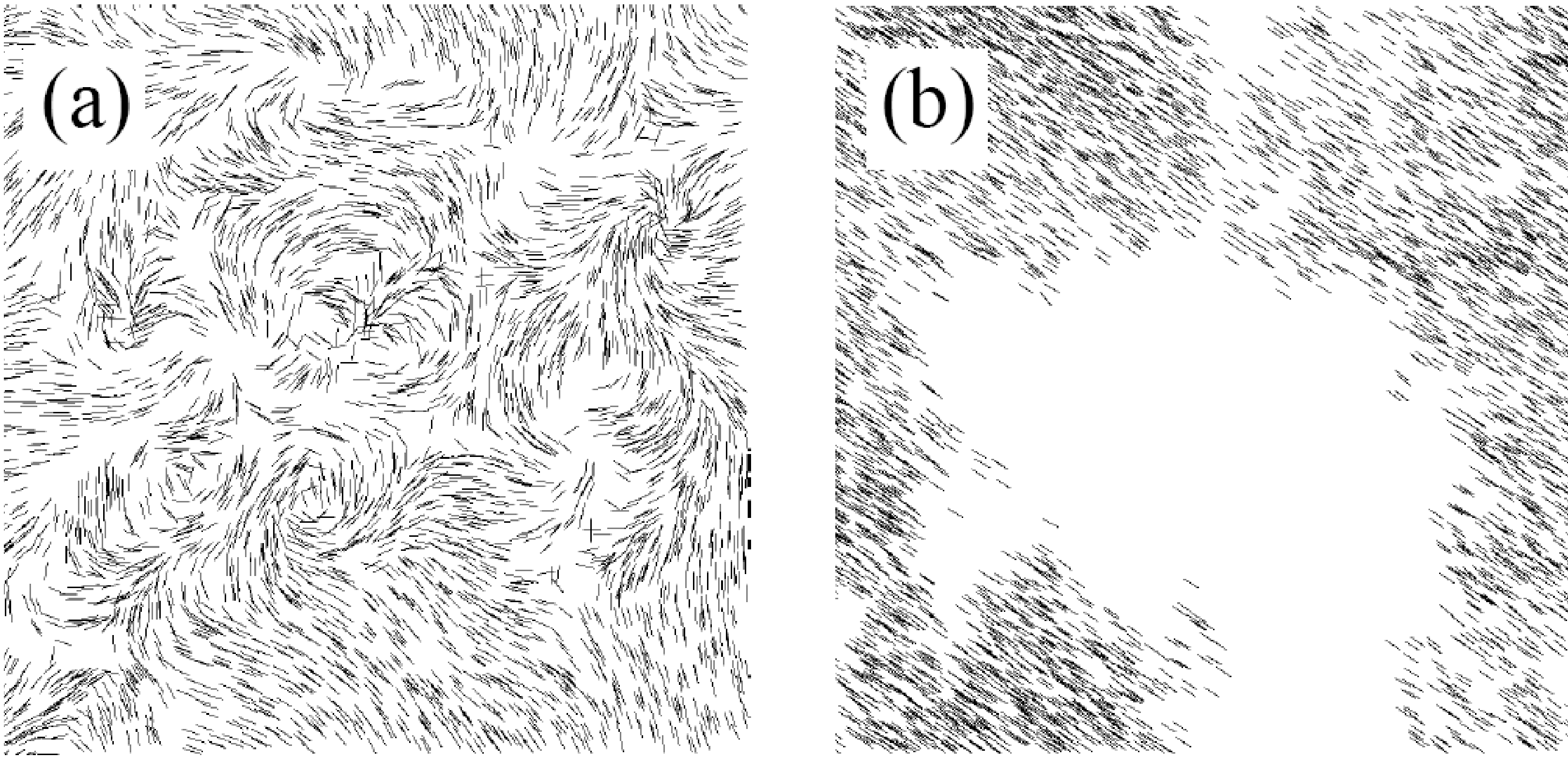
noise (error)

local average velocity



Vicsek *et al.*, (1995)

Locust hopper bands



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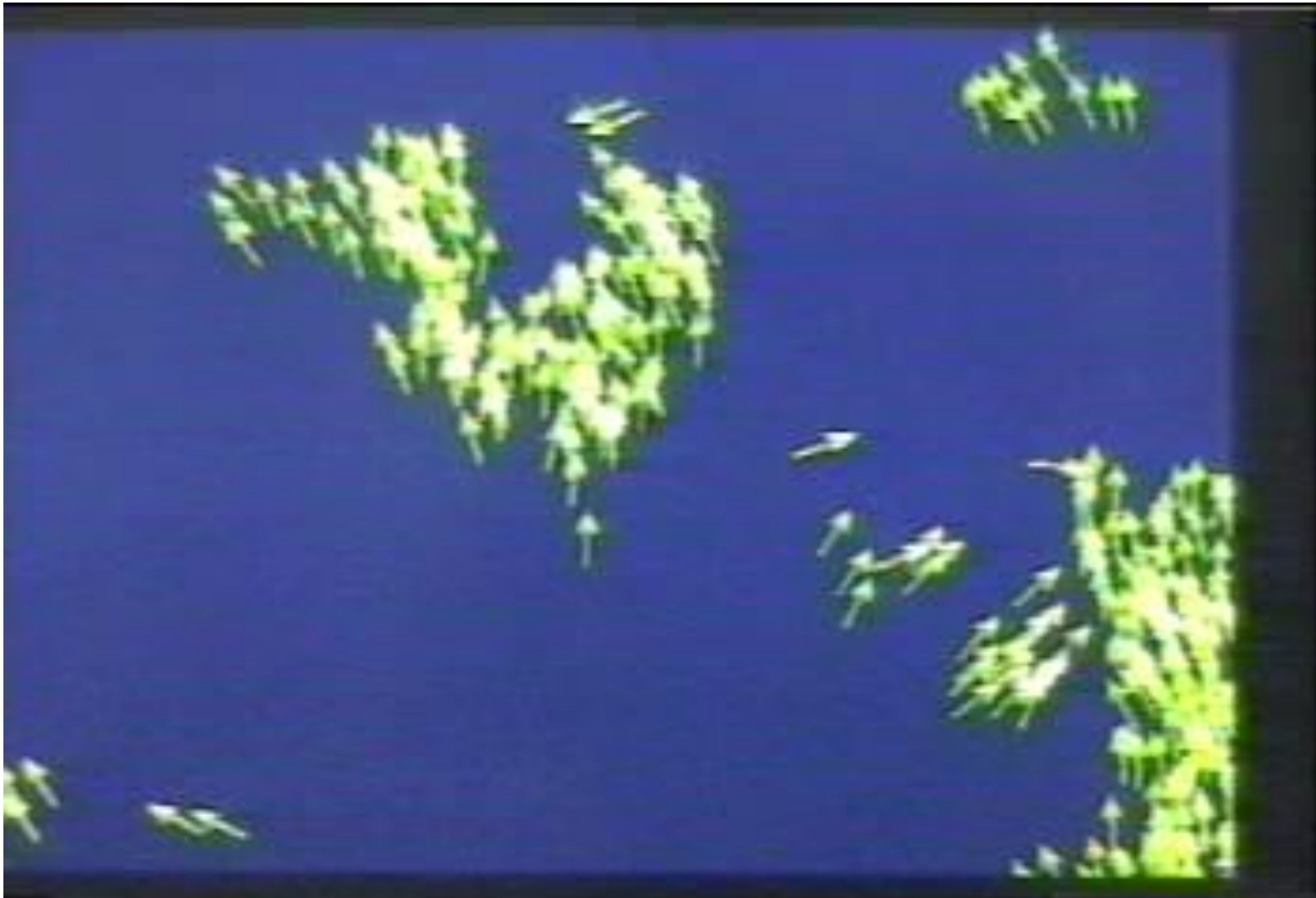
Locust hopper bands



Vicsek *et al.*, (1995)

Locust hopper bands

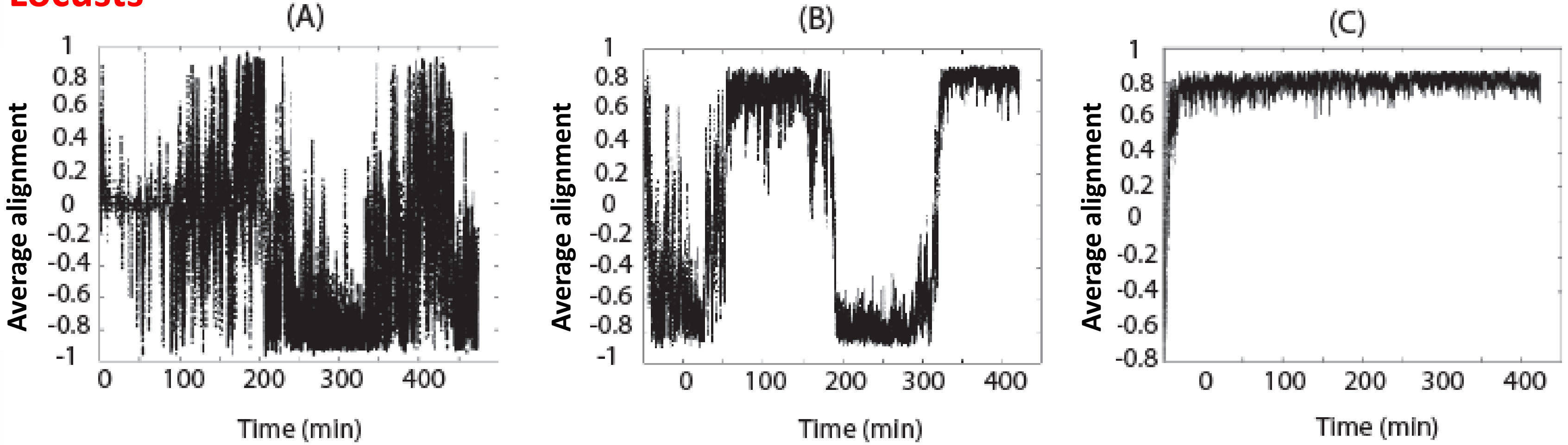
Increasing density

(like gas)

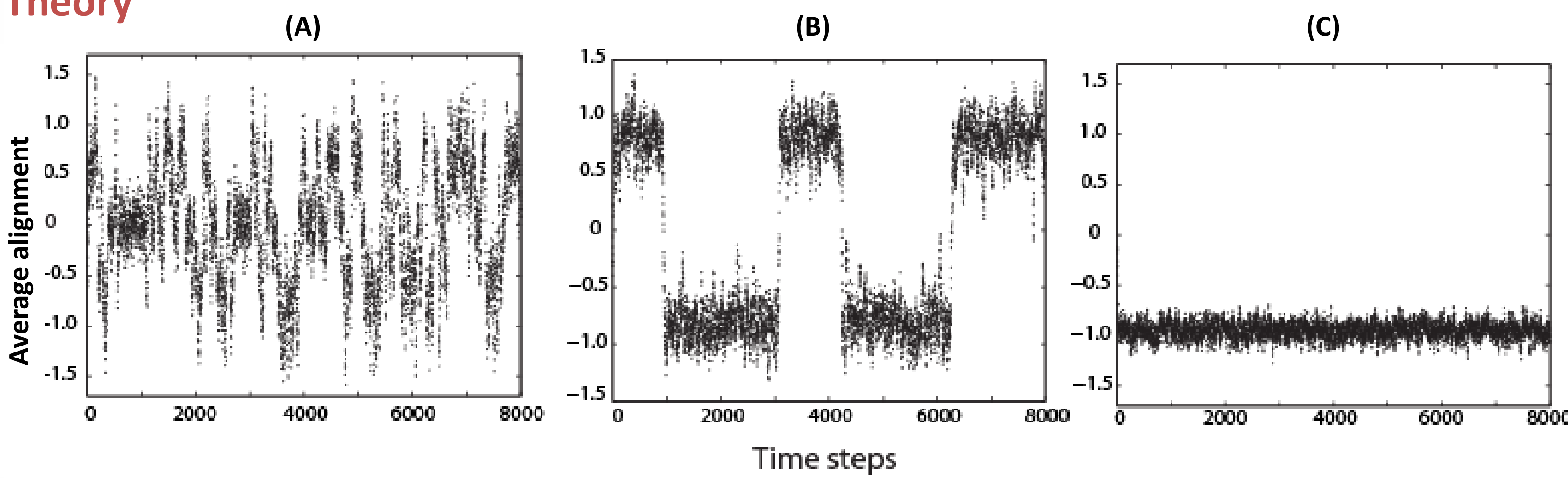
(near transition state)

(ordered phase: driven liquid)

Locusts

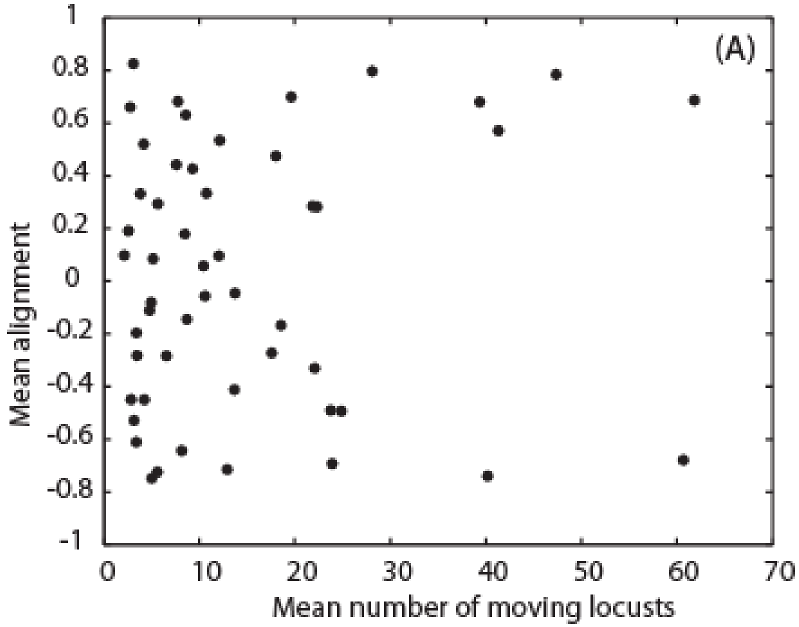


Theory



Locust hopper bands

Locusts



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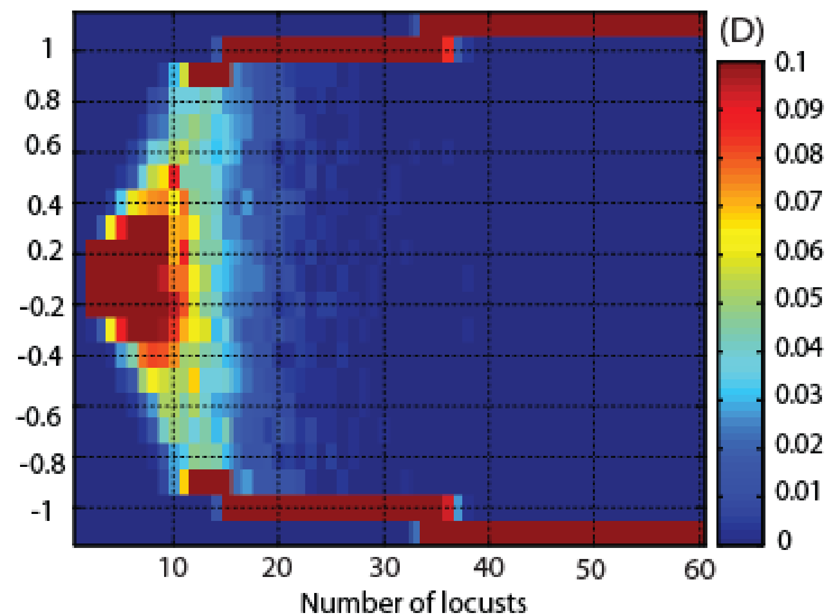
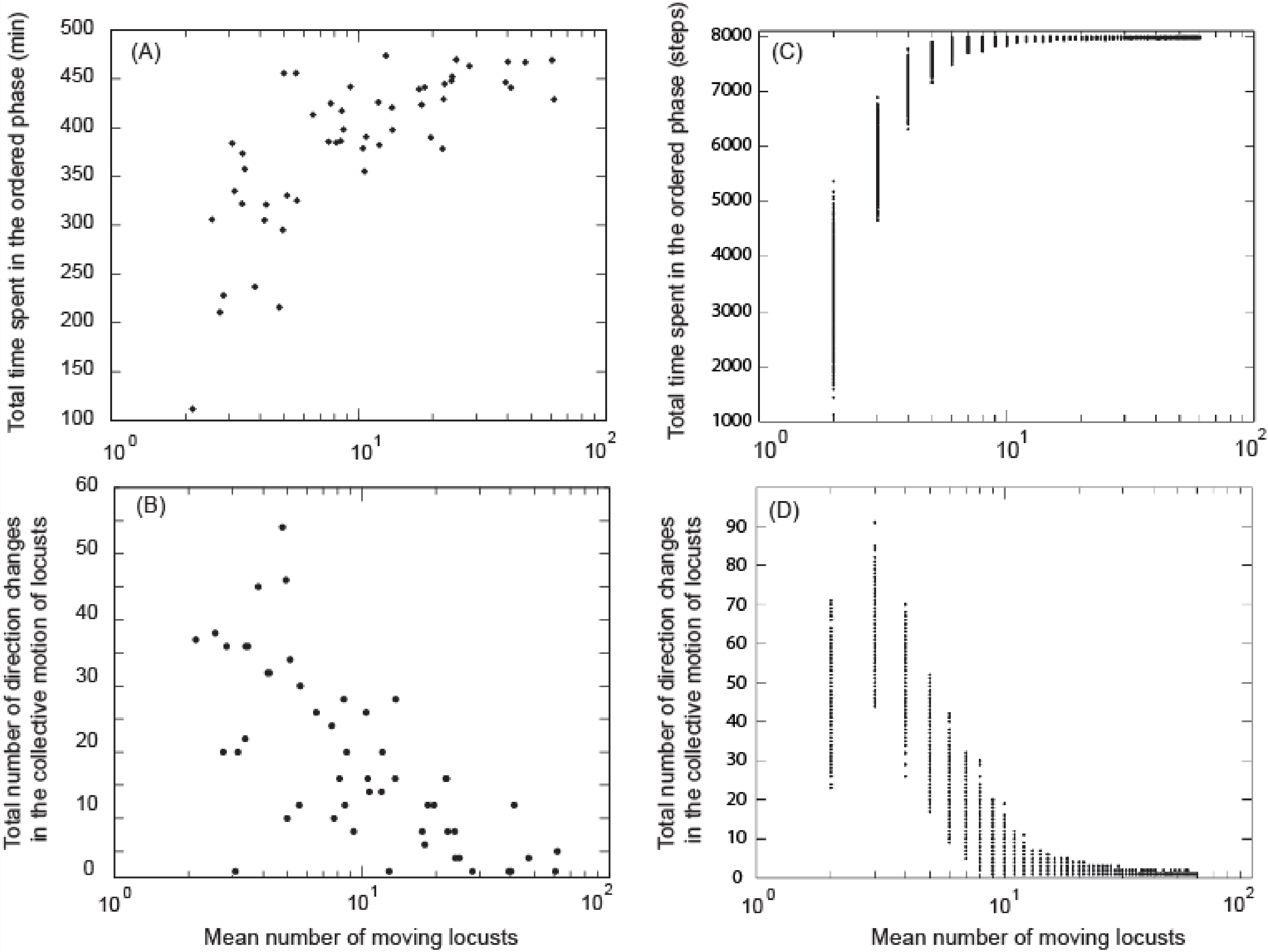


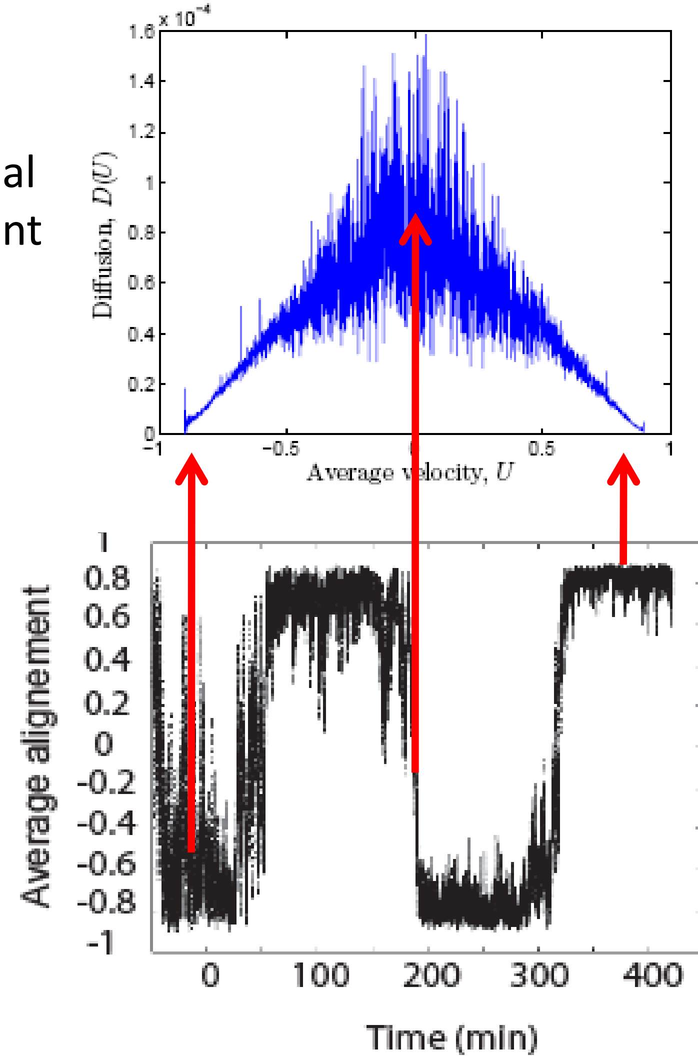
Locust hopper bands

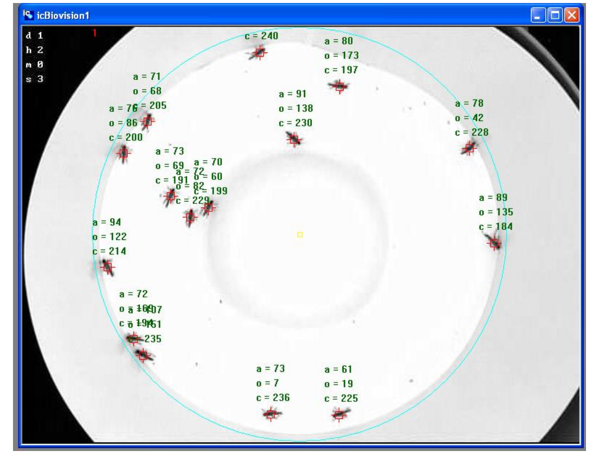
Locusts | **Theory**

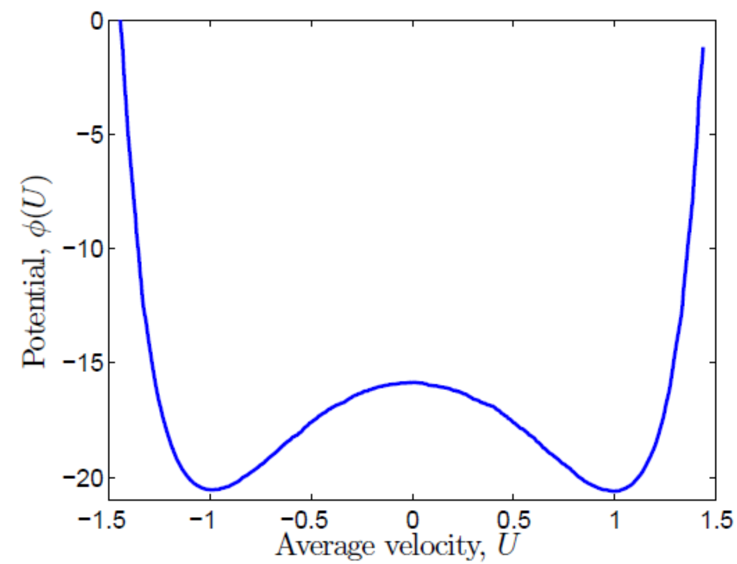


Locust hopper bands

Individual Movement Error







"Inherent noise can facilitate coherence in collective swarm motion"
PNAS (2009) **106**(14), 5464-5469.

Sepideh Bazazi & Jerome Buhl

Locust hopper bands

an extremely selfish herd

Current Biology (2008) **18**(10), 735-739.

Cannibalism and collective motion

with Sepideh Bazazi & Jerome Buhl

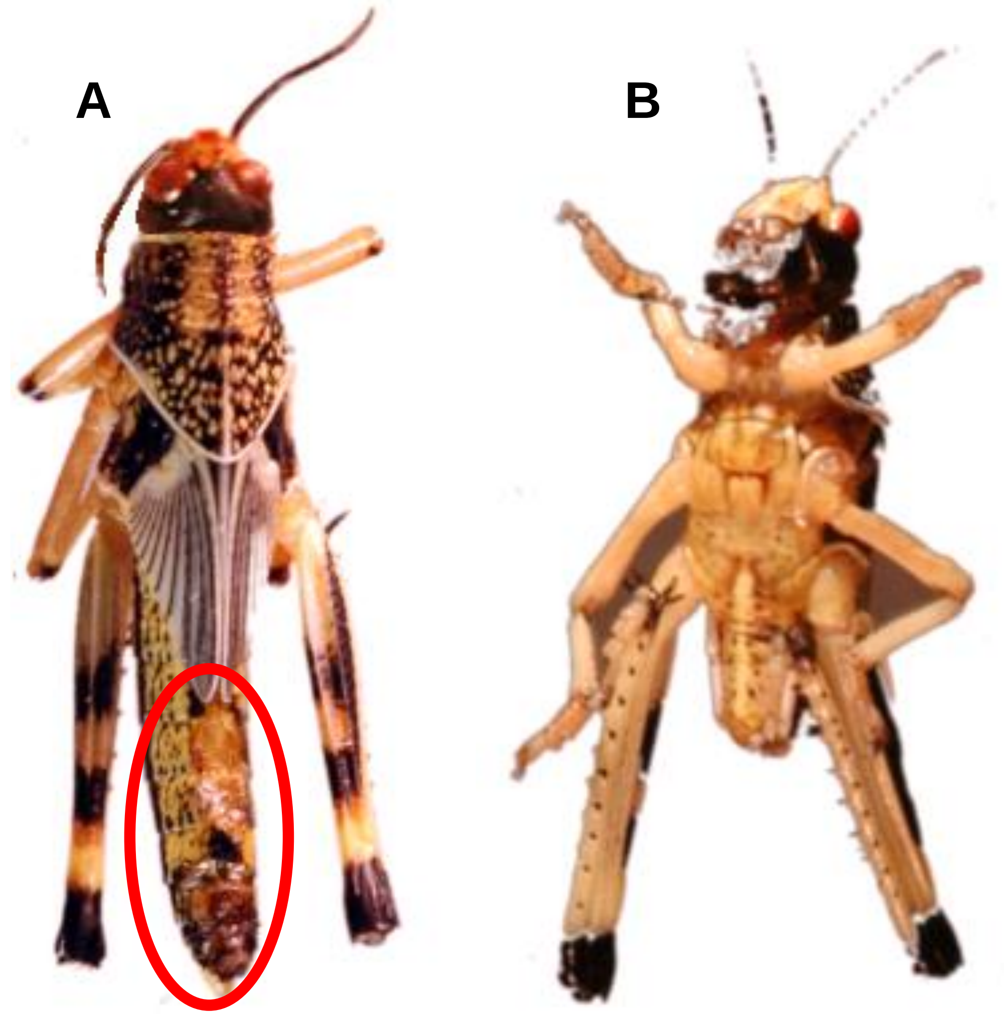
Aggressive interactions

0 2 4 6

Time (seconds)

with Sepideh Bazazi & Jerome Buhl

Aggressive interactions

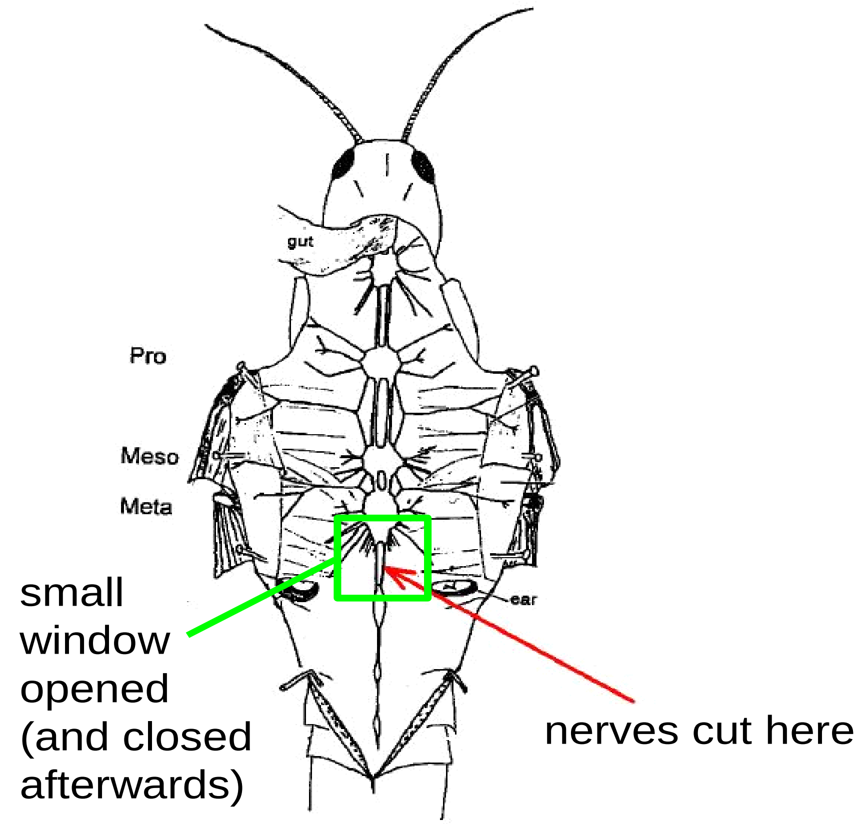


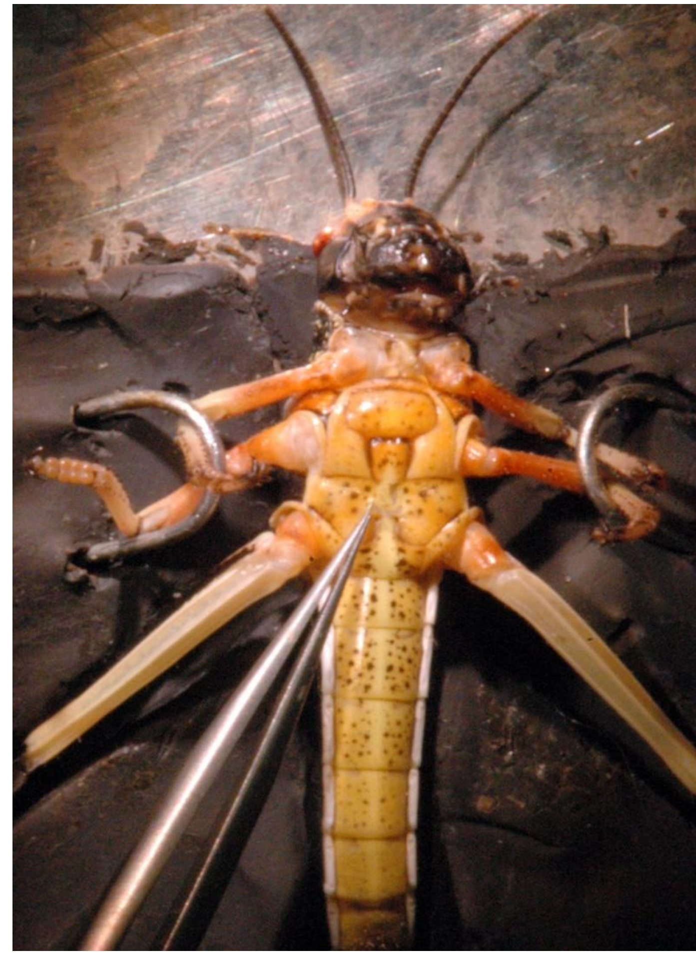
Cannibalism and collective motion

with Sepideh Bazazi & Jerome Buhl

Removing sensation from the abdomen

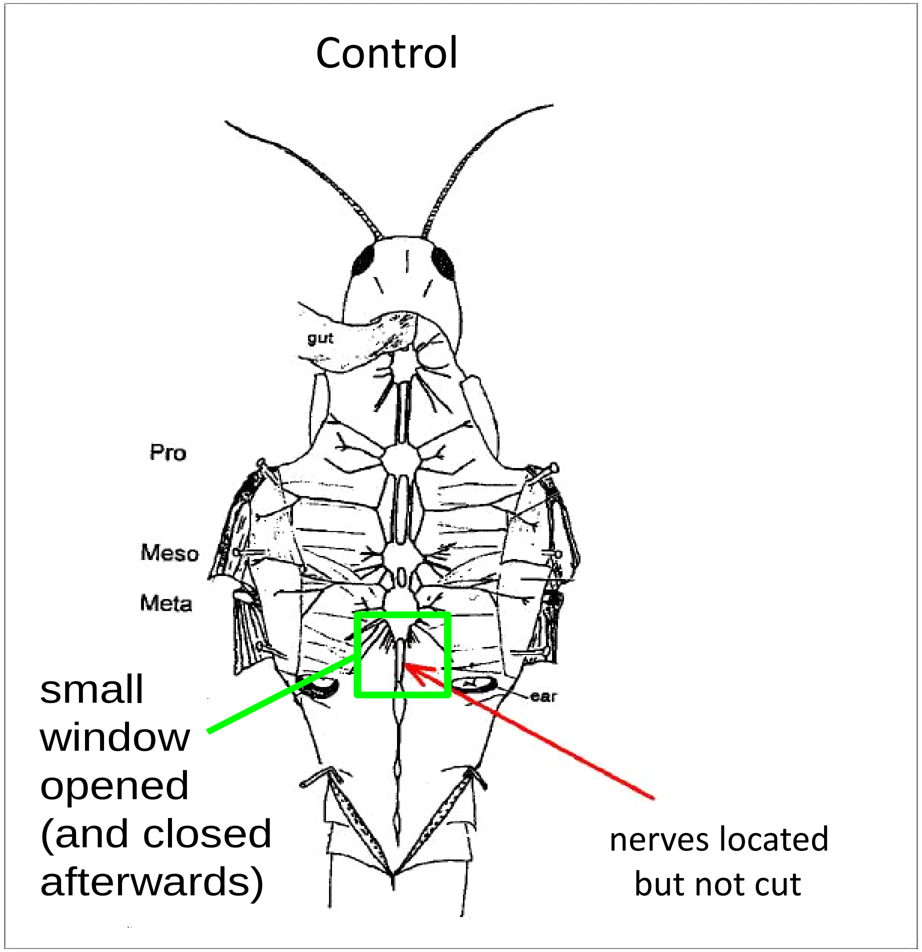
Nerve cut

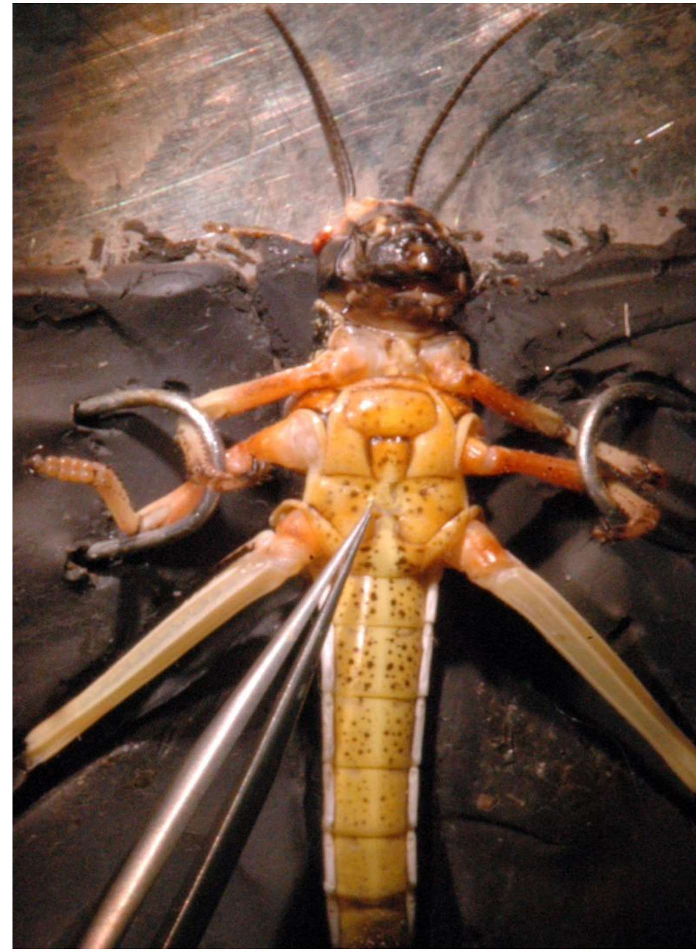




with Sepideh Bazazi & Jerome Buhl

Removing sensation from the abdomen

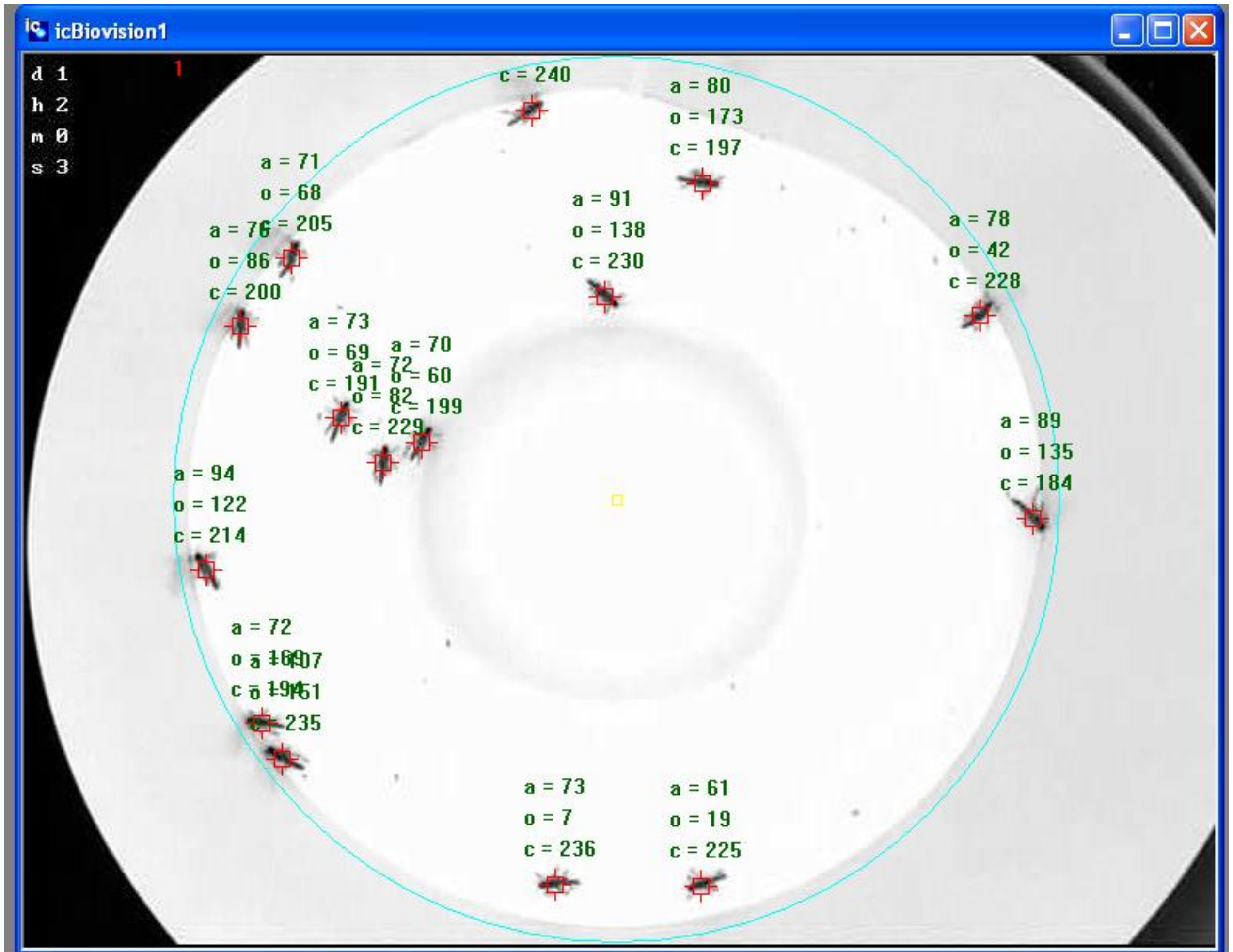




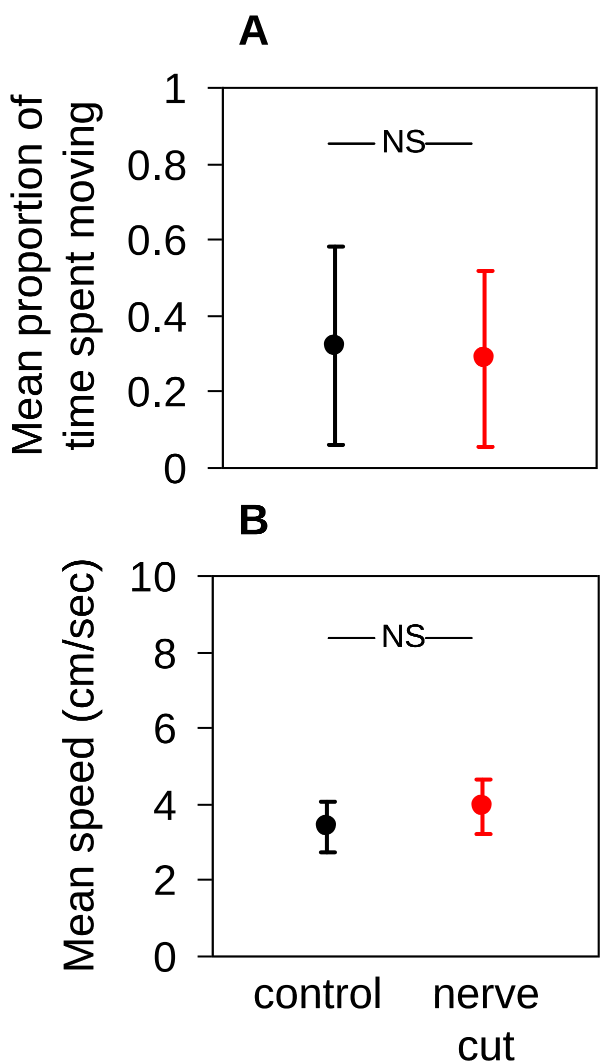
with Sepideh Bazazi & Jerome Buhl

Cannibalism and collective motion

Do they influence collective motion?



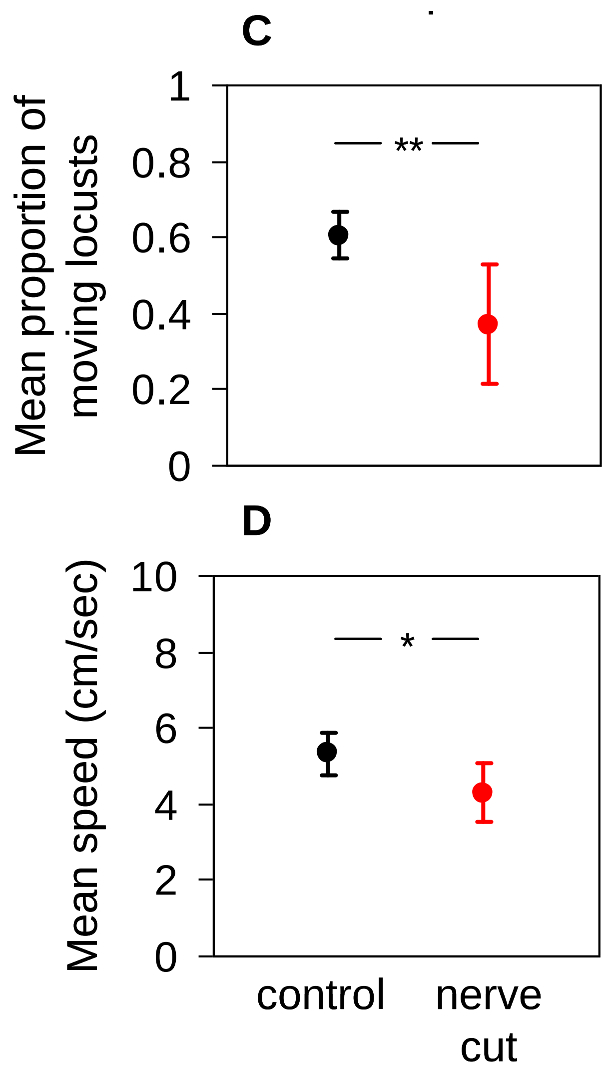
Isolated individuals



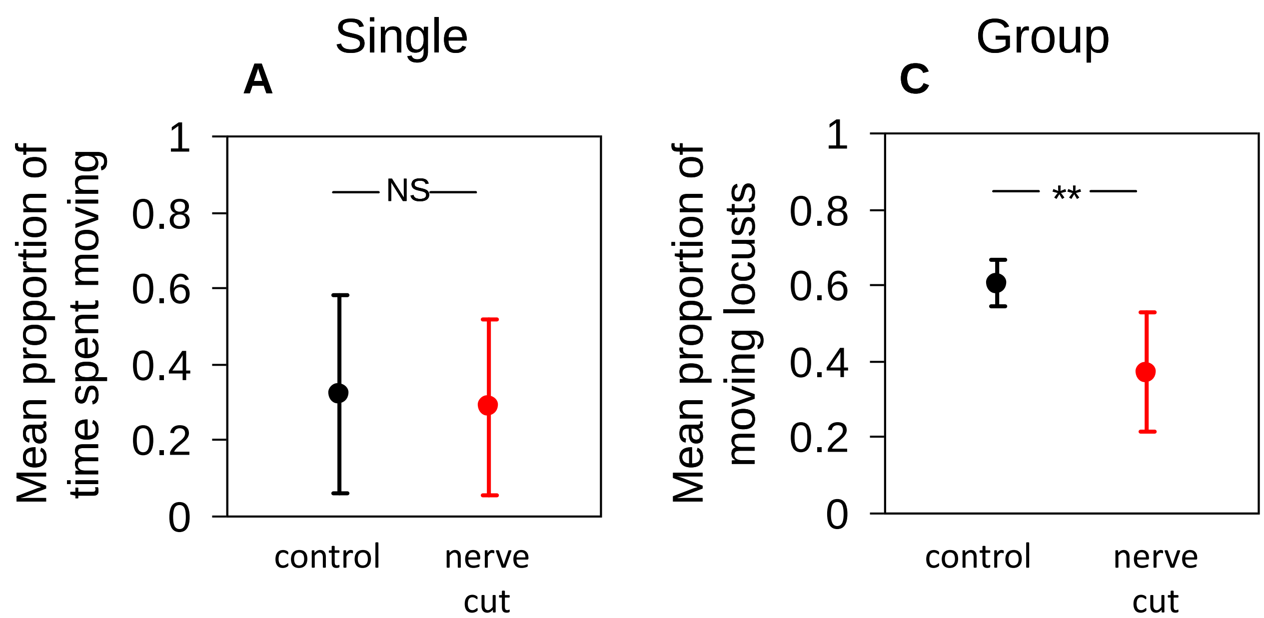
No difference in behaviour

Cannibalism and collective motion

Collective motion of groups

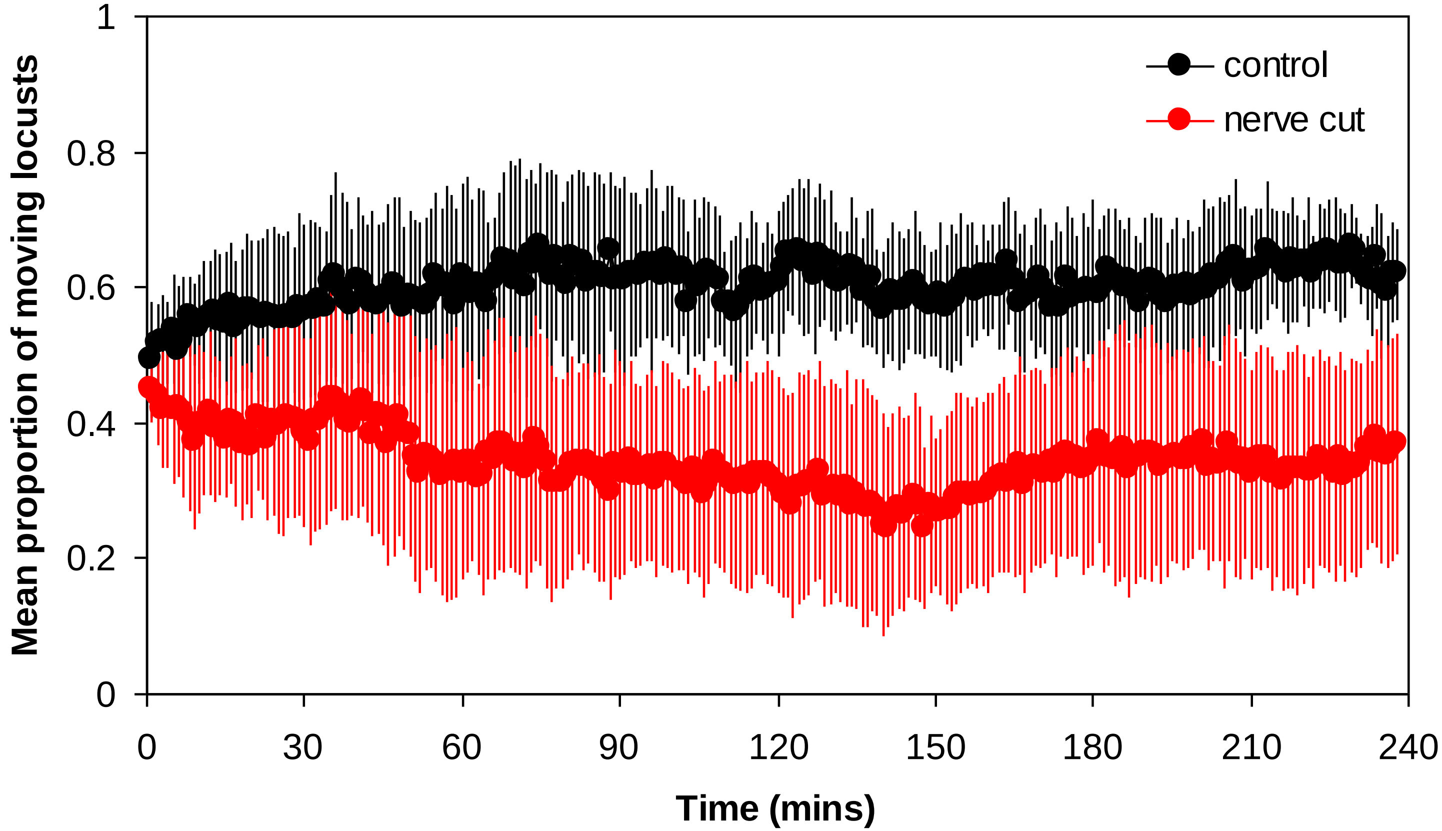


Cannibalism and collective motion

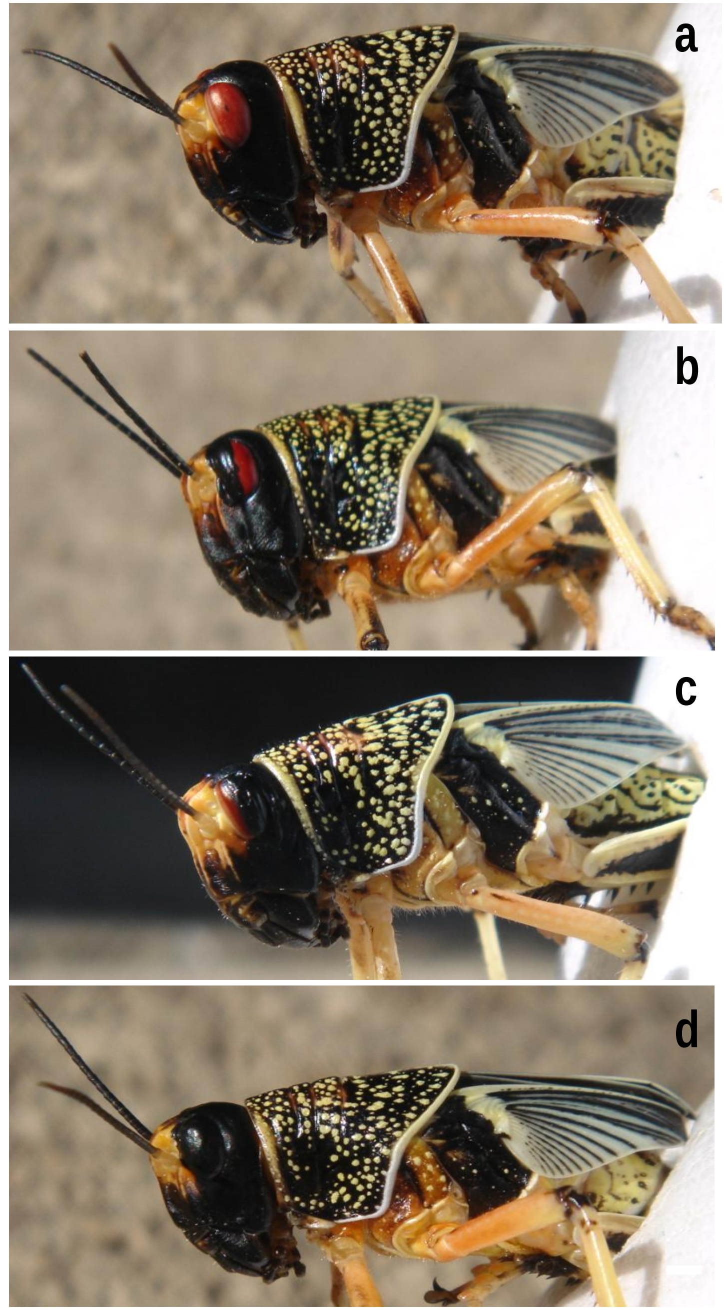


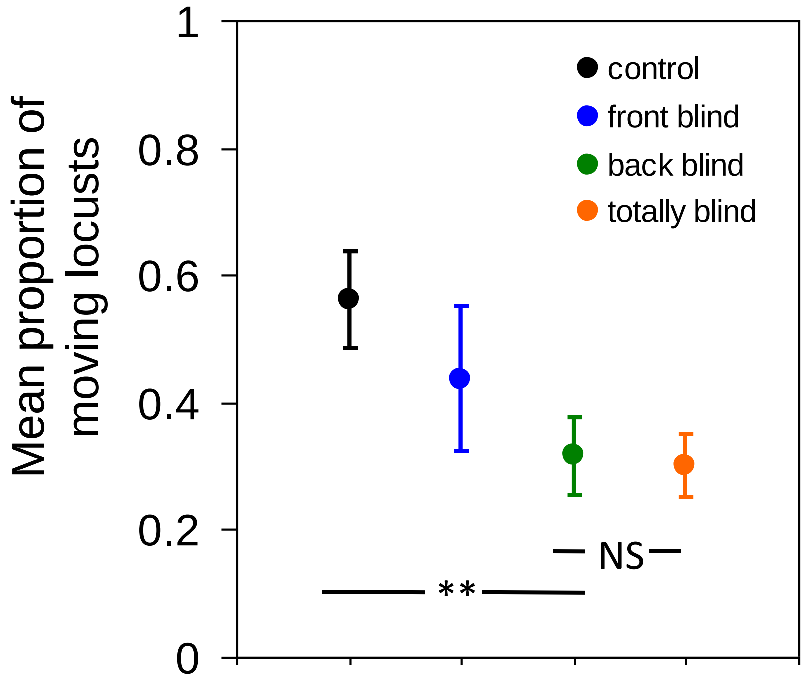
Cannibalism and collective motion

Time series of group experiments



Visual system

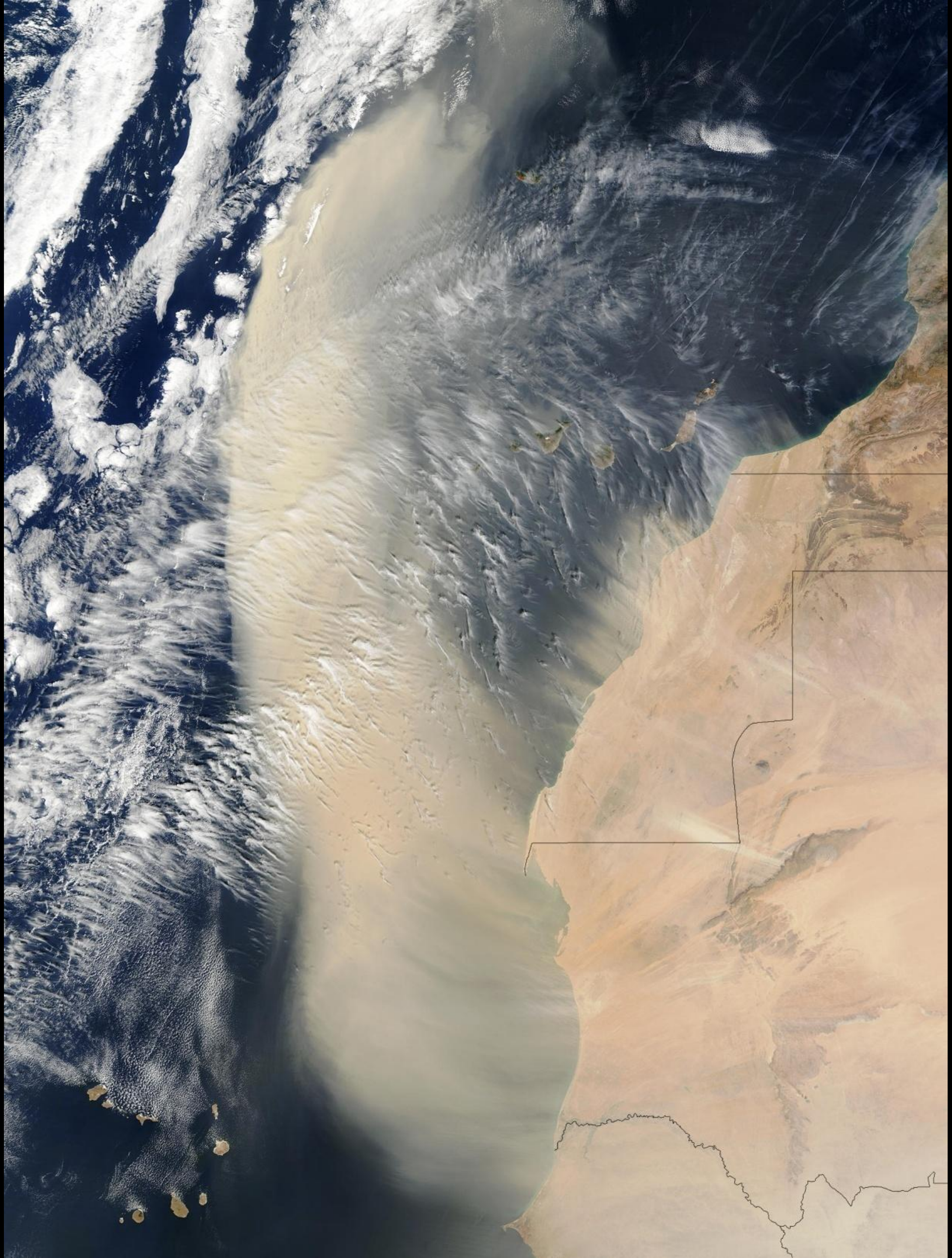

a
b
c
d


Mean proportion of moving locusts
1
0.8
0.6
0.4
0.2
0
control
front blind
back blind
totally blind
NS
**

When locust density increases it is *aggressive interactions* among individuals that is the dominant factor in the onset of collective motion

Collective mass migration of locust hoppers, far from being cooperative act, is in effect a *forced march*


Field experiments



Mormon Crickets

Field experiments

Collaborators: Steve Simpson, Greg Sword, Pat Lorch

Proc. Natl. Acad. Sci. USA (2006) **103**, 4152-4156

Locust hopper bands

Mormon Crickets

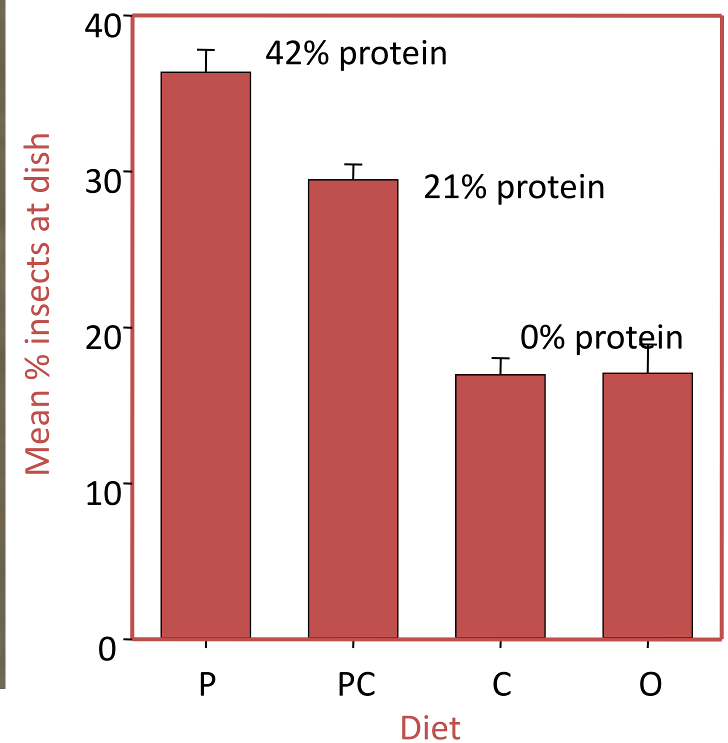
Locust hopper bands

Locust hopper bands

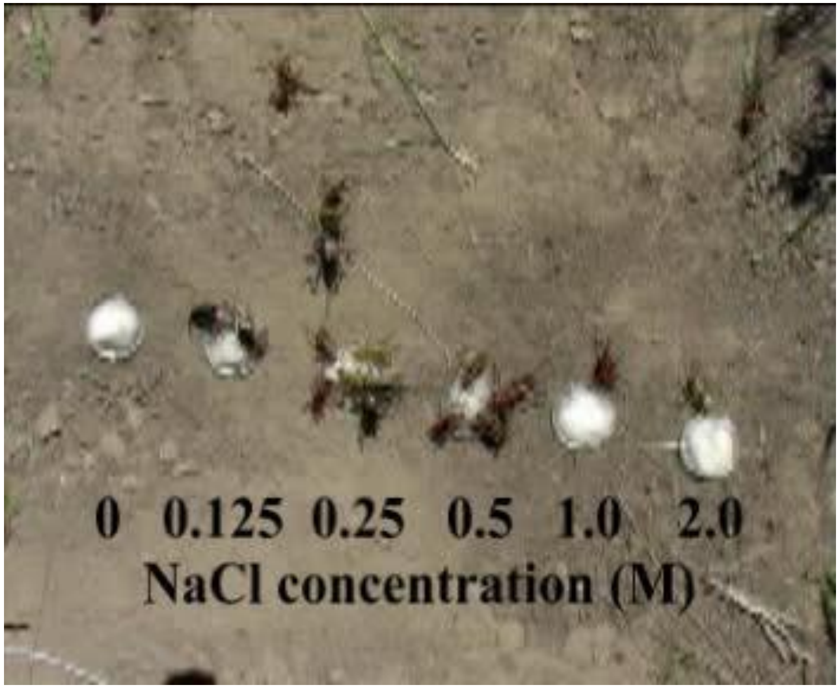
Locust hopper bands

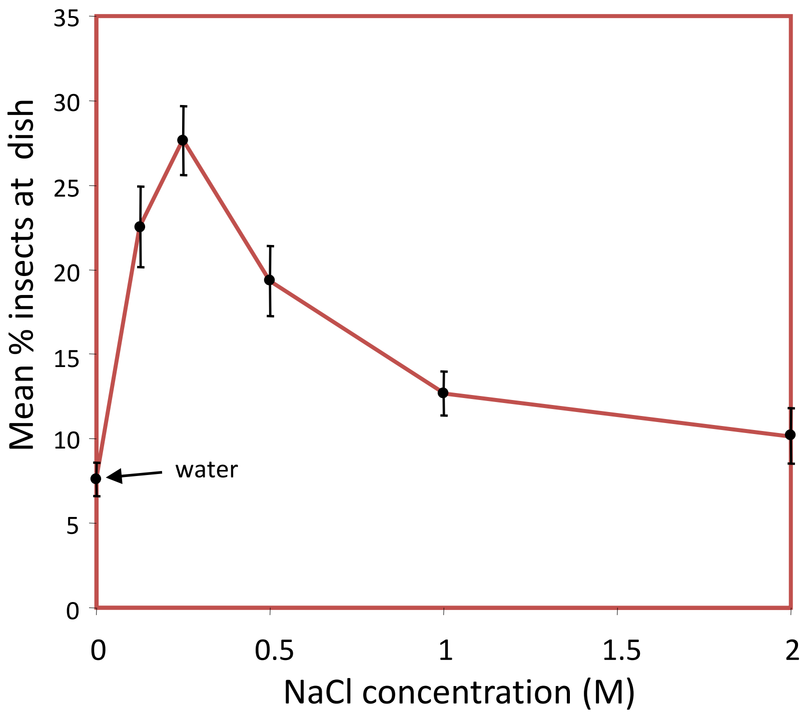
Locust hopper bands

Locust hopper bands



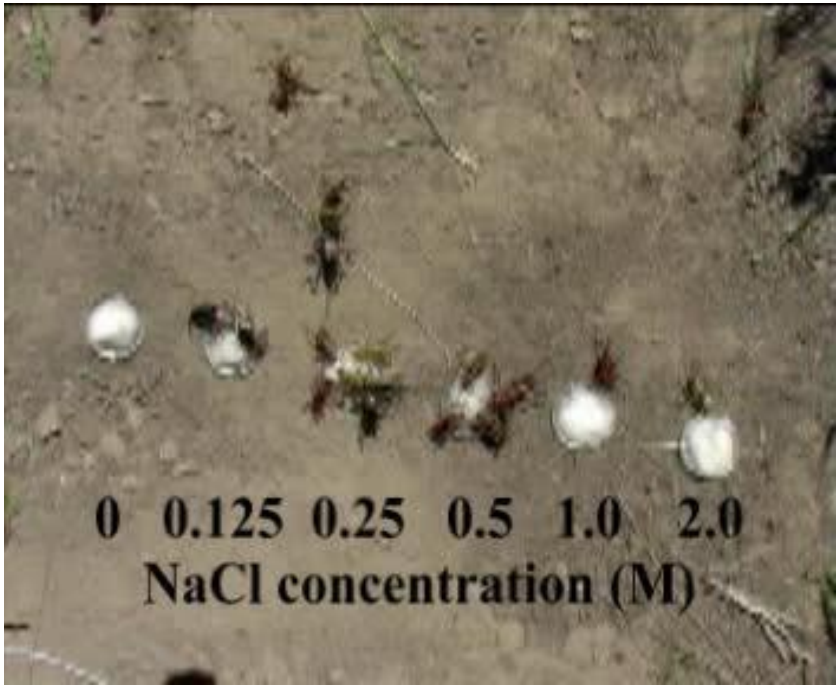
Locust hopper bands

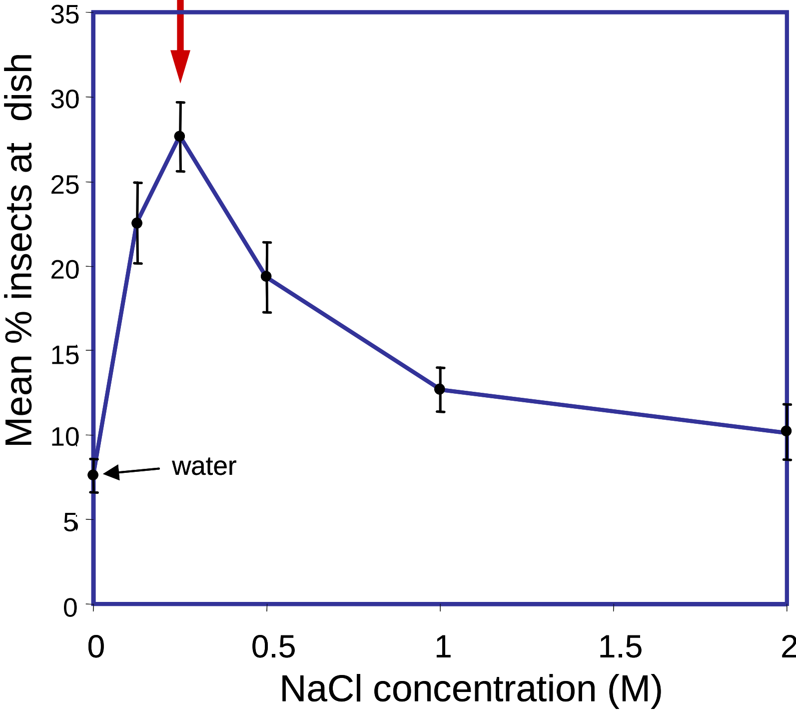




Locust hopper bands

concentration of cricket blood





Locust hopper bands

The forced march

Individuals attack those ahead and try to prevent being attacked from behind

Locust hopper bands

The forced march

Individuals attack those ahead and try to prevent being attacked from behind

Stop and you risk being cannibalised

The forced march

Predictions

Protein and salt satiation should reduce cannibalism

…and inhibit marching

The forced march

Predictions

Protein and salt satiation should reduce cannibalism

Protein or salt satiated crickets cannibalised 30-50% less ($P<0.0005$)

…and inhibit marching

Protein-satiated crickets spent ~50% less time walking than protein-deprived insects ($P< 0.006$)

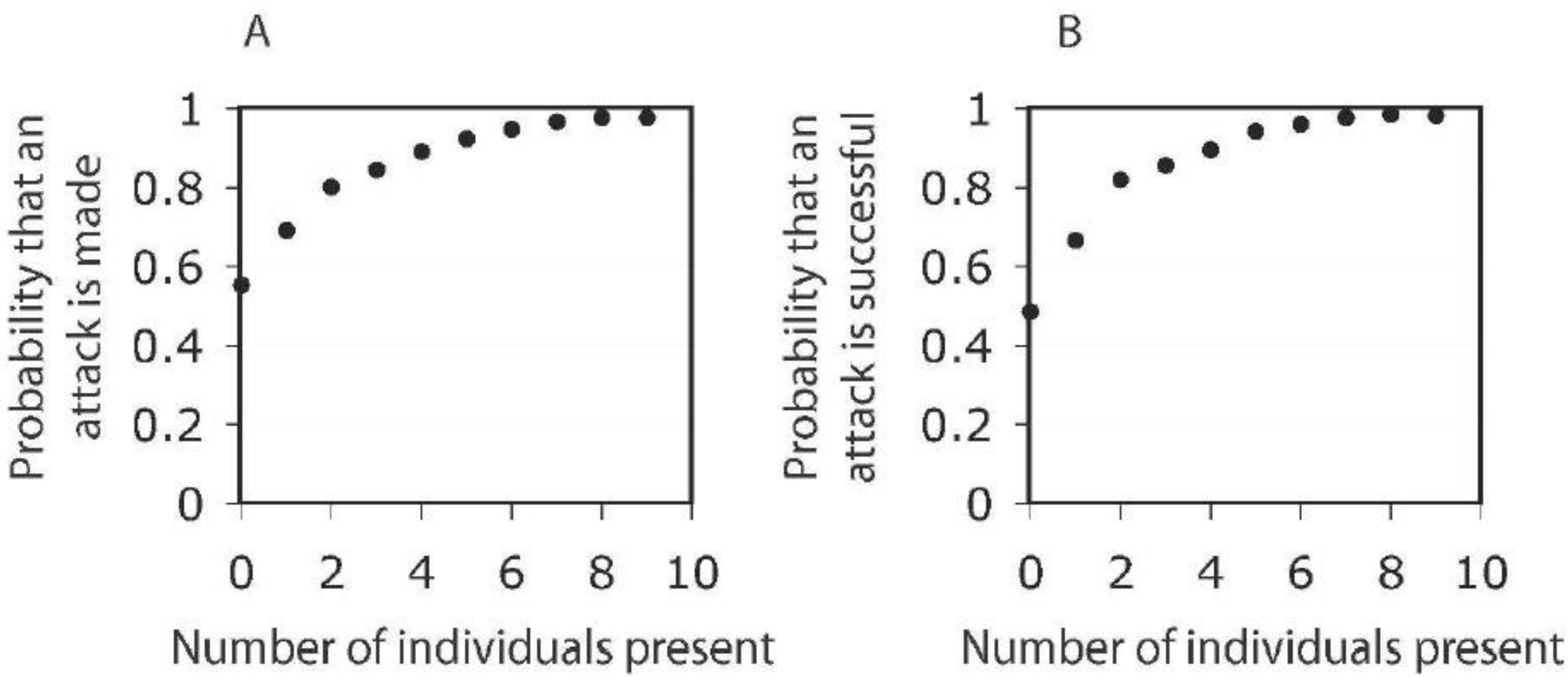
Locust hopper bands

The forced march

Cannibalism is socially facilitated

Bazazi *et al*. (2010), in revision

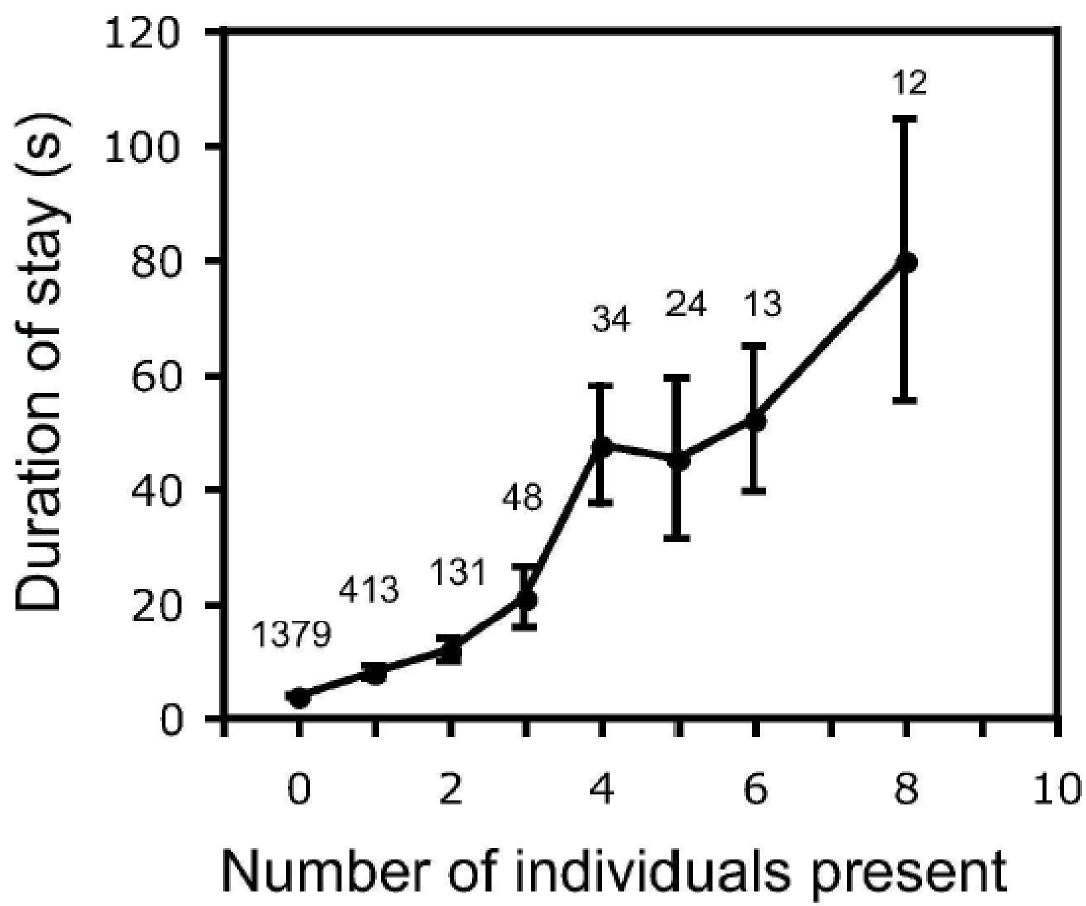
The forced march



Bazazi *et al*. (2010), in revision

Locust hopper bands

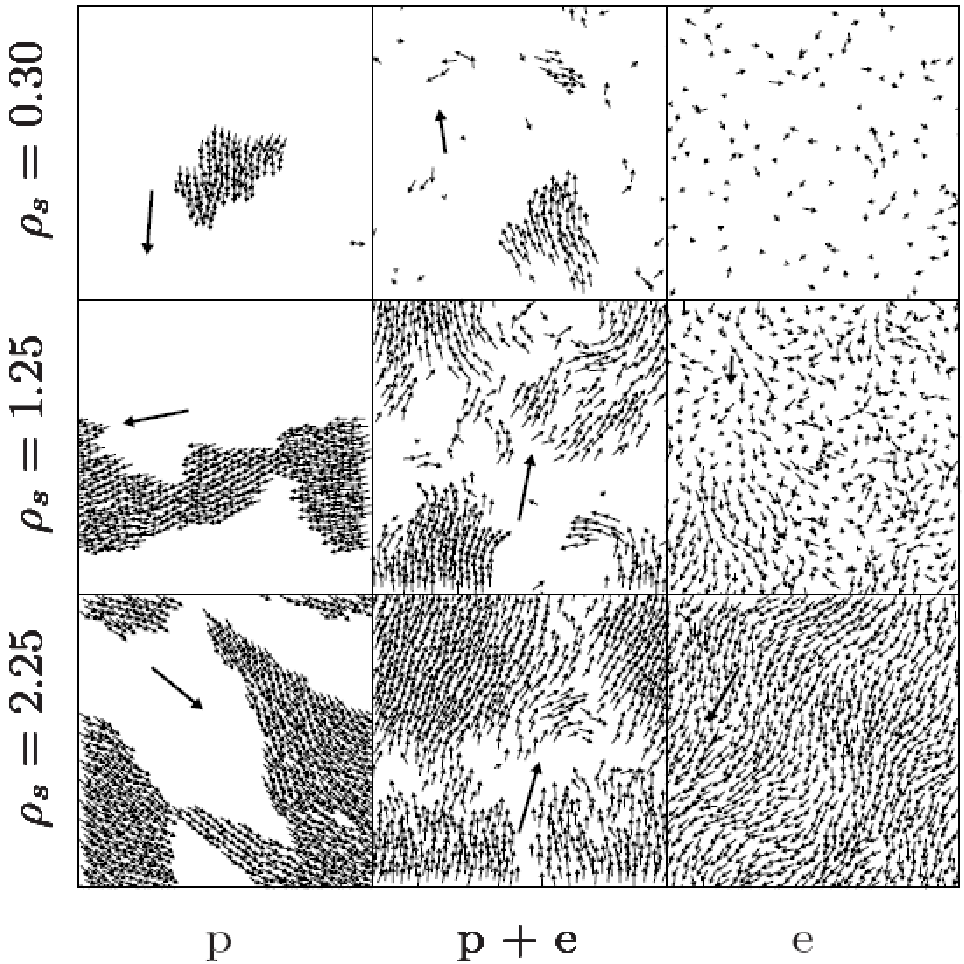
The forced march

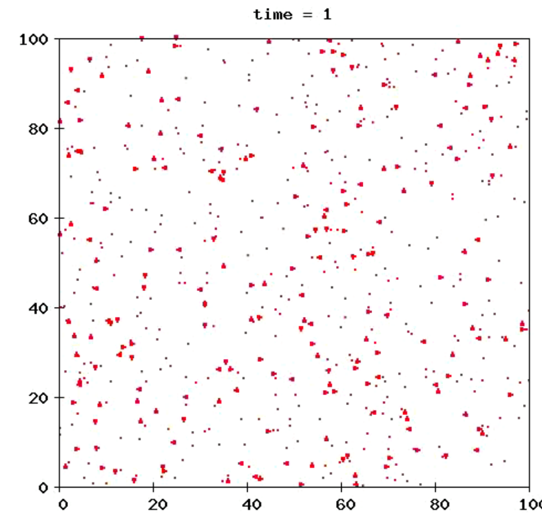


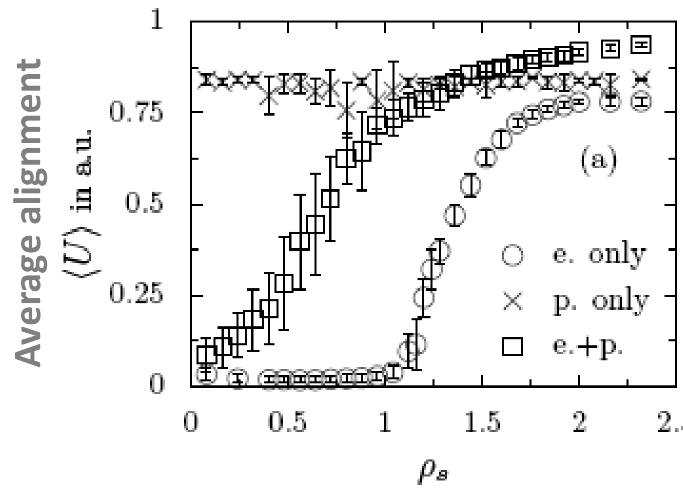
Bazazi *et al*. (2010), in revision

Locust hopper bands

with Pawel Romanczuk & Lutz Shimansky-Geier

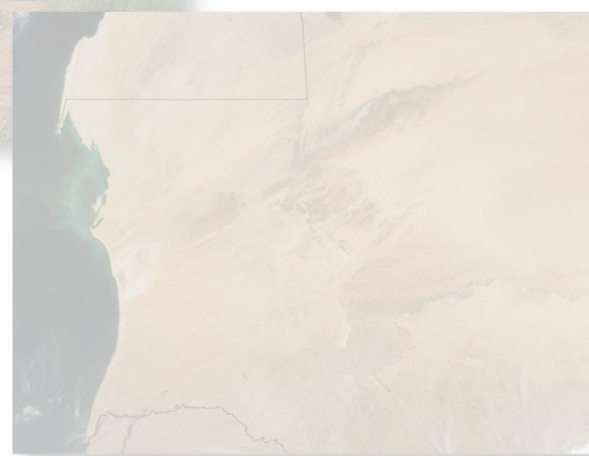






Physical Review Letters (2009)

Lab and field experiments / modeling



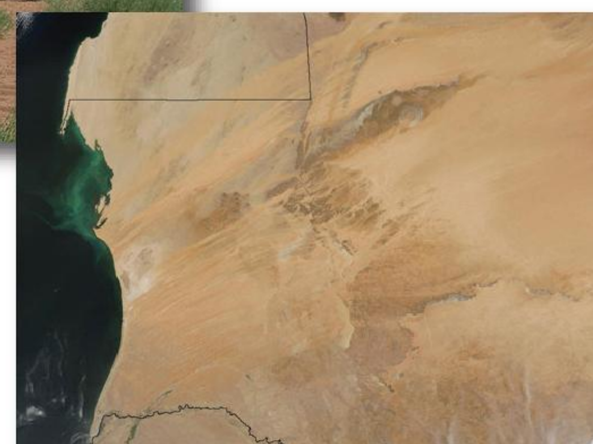
-statistical physics
-nutritional ecology
-landscape ecology
-neurobiology
-physiology
-evolutionary modeling

Lab and field experiments / modeling

Field surveys / aerial photography
desert vegetation models

Lab and field experiments / modeling

Field surveys / aerial photography
desert vegetation models



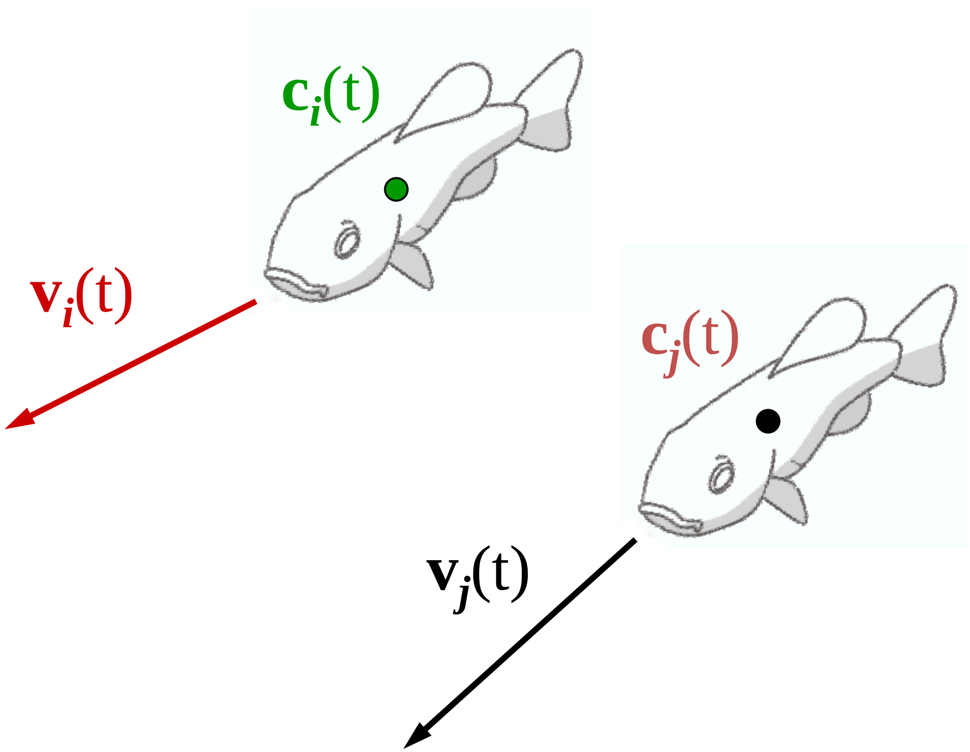
Satellite images of known outbreak areas
GPS data of swarm locations
Demographic data

Climate models
High-performance computation

Locust hopper bands

Will return to discuss the evolution of mass migration

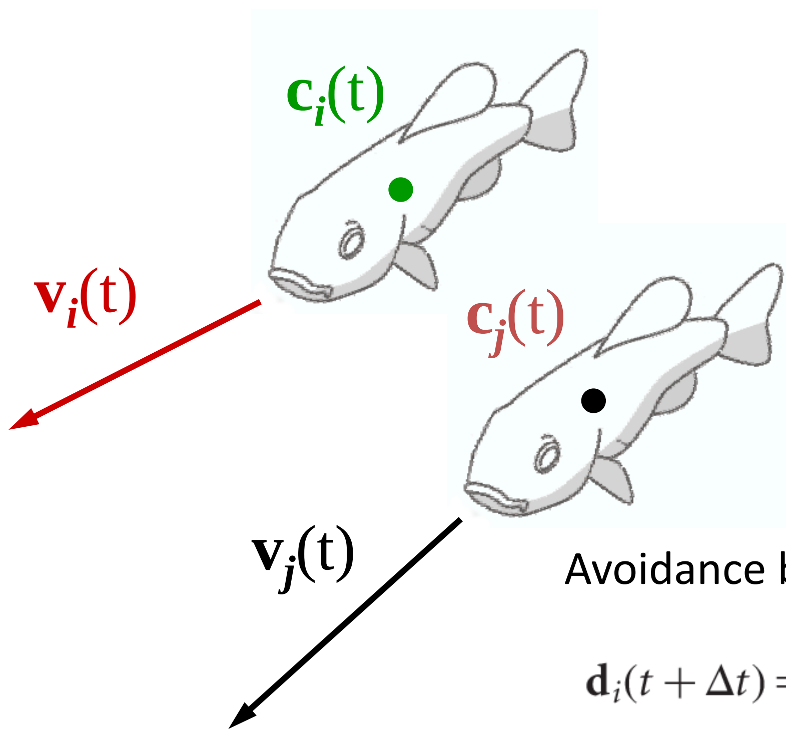
Equations of motion



Journal of Theoretical Biology (2002) **218**, 1-11

Group motion and collective memory

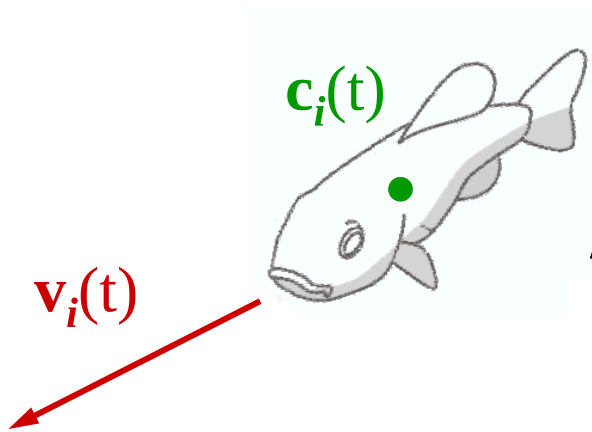
Equations of motion



Avoidance behaviour (repulsion)

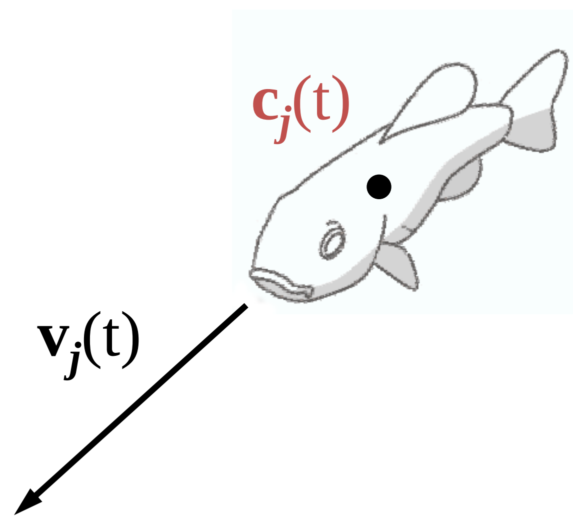
$$\mathbf{d}_i(t+\Delta t) = -\sum_{j\neq i} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{|(\mathbf{c}_j(t) - \mathbf{c}_i(t))|}$$

Equations of motion



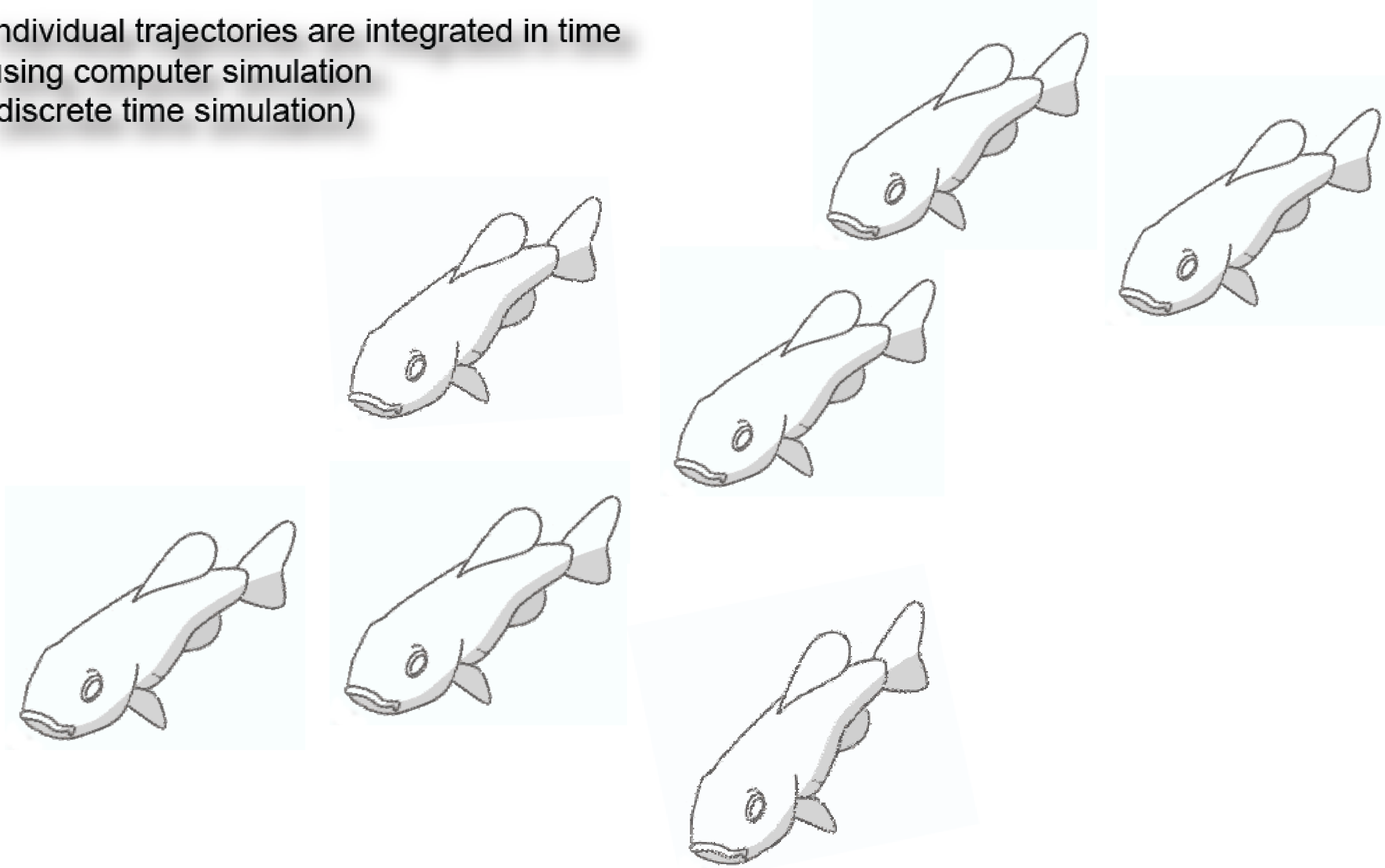
Attraction and/or alignment of direction

$$\mathbf{d}_i(t+\Delta t) = \sum_{j \neq i} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{|(\mathbf{c}_j(t) - \mathbf{c}_i(t))|} + \sum_{j=1} \frac{\mathbf{v}_j(t)}{|\mathbf{v}_j(t)|}$$

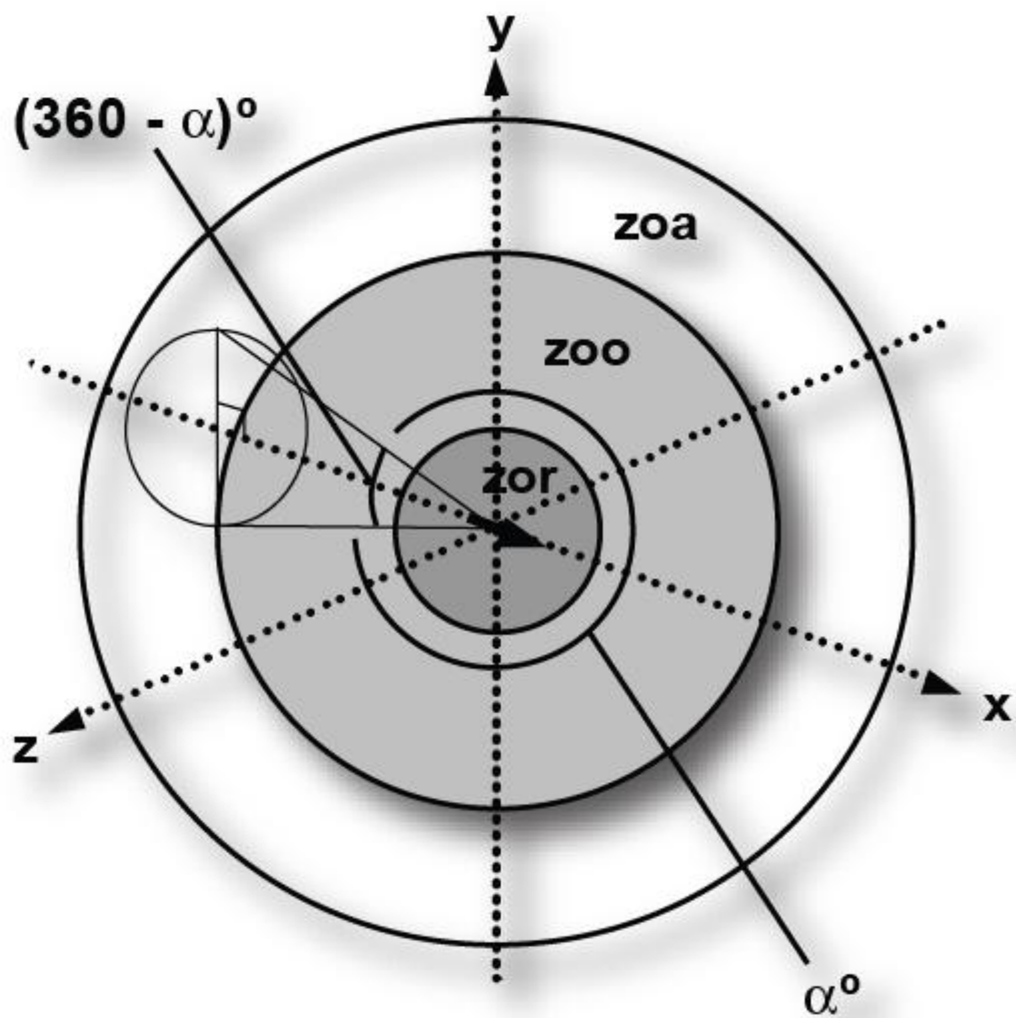


Equations of motion

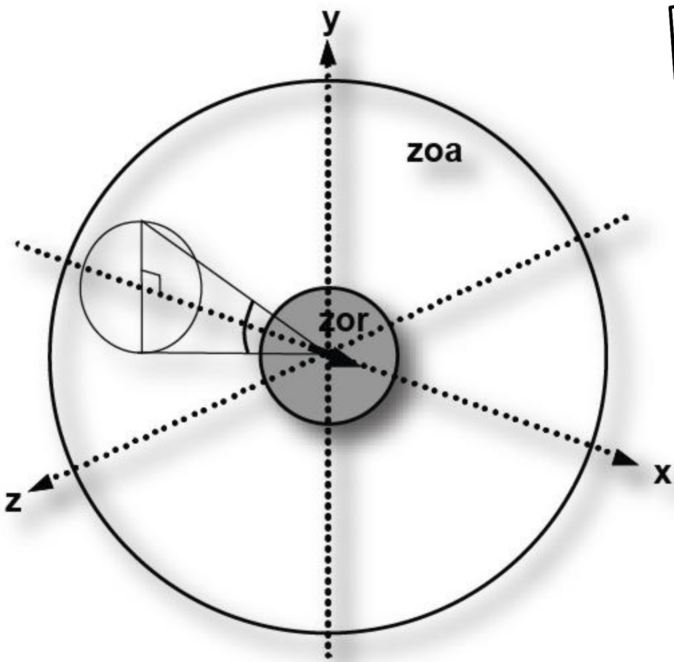
Individual trajectories are integrated in time
using computer simulation
(discrete time simulation)

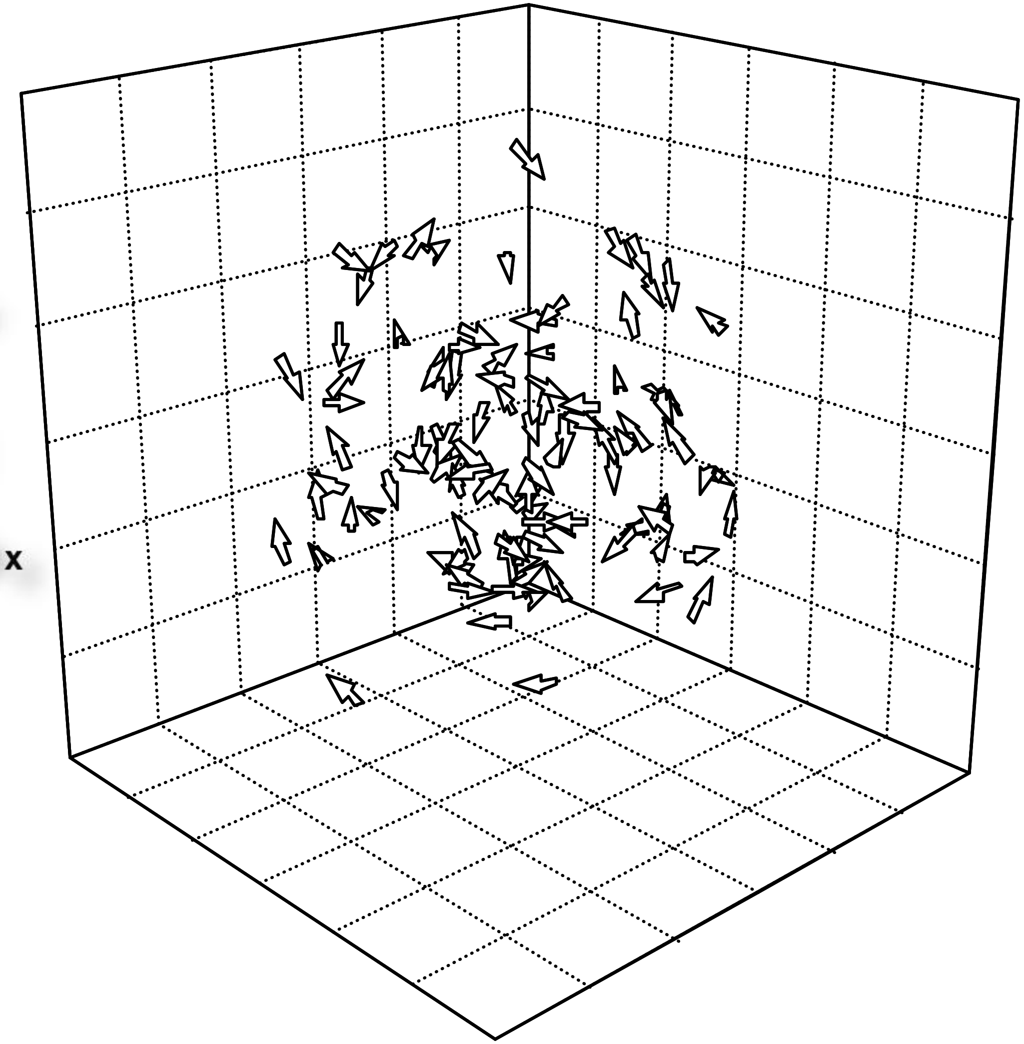


Group motion and collective memory

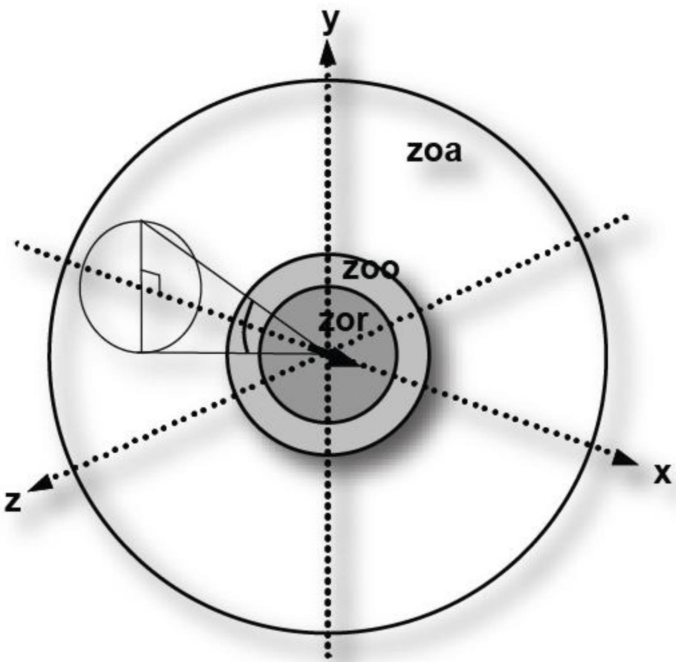


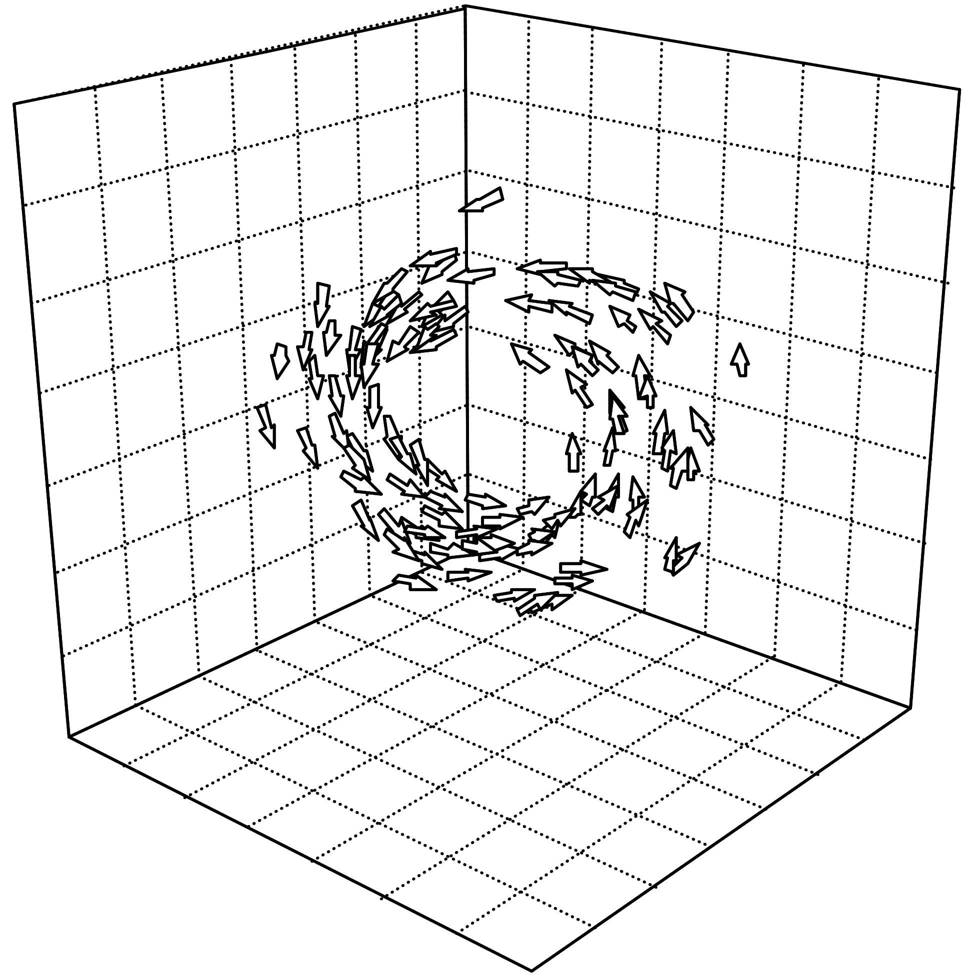
Group motion and collective memory



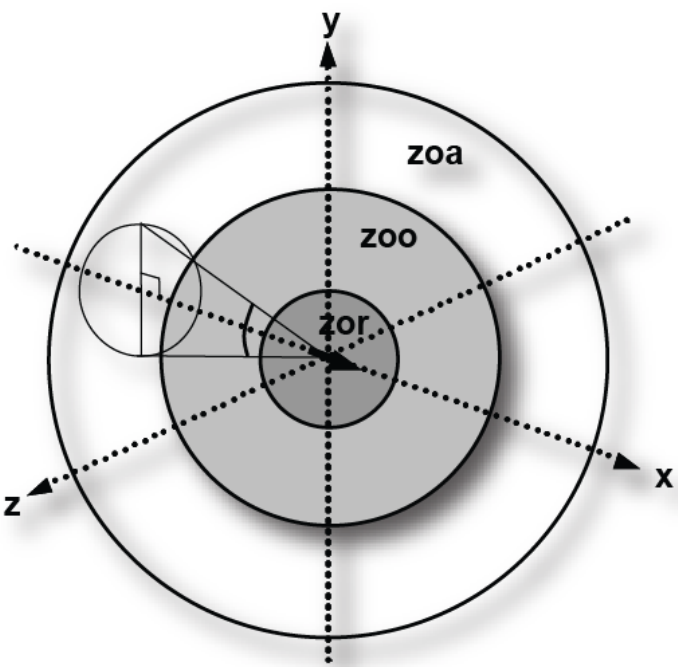


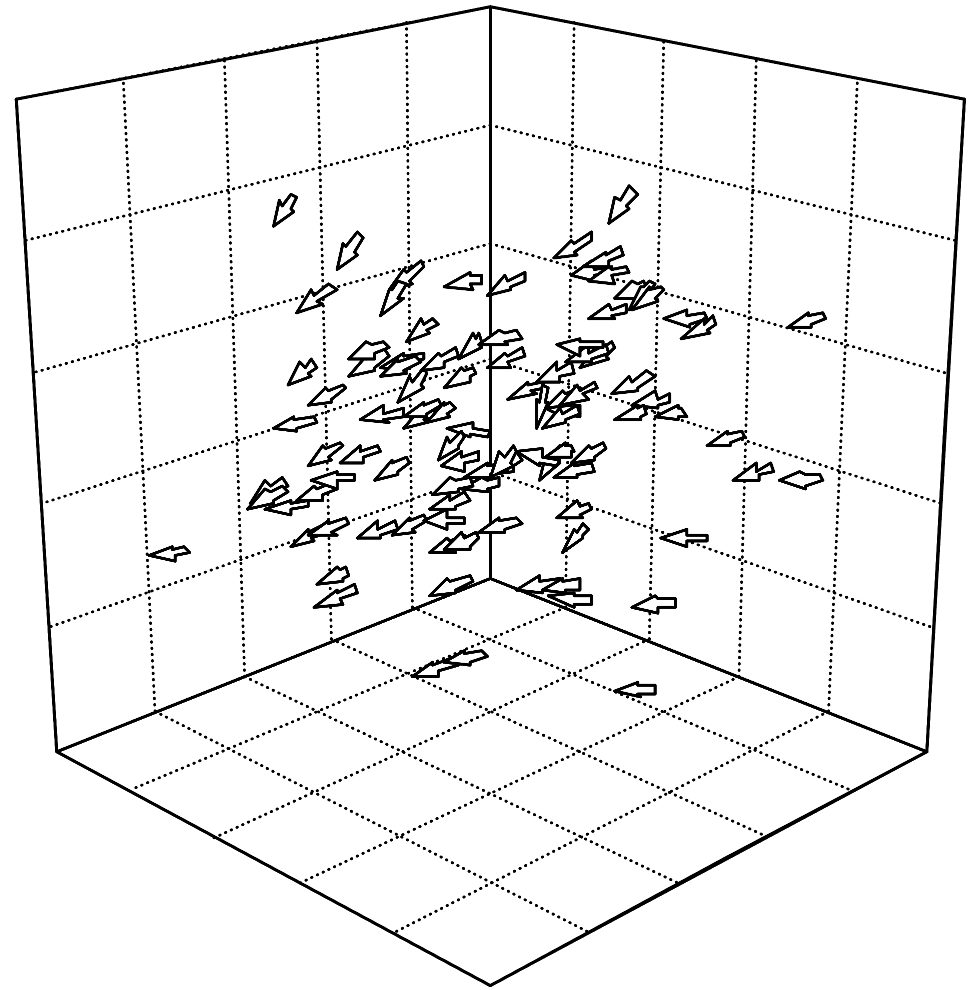
Group motion and collective memory



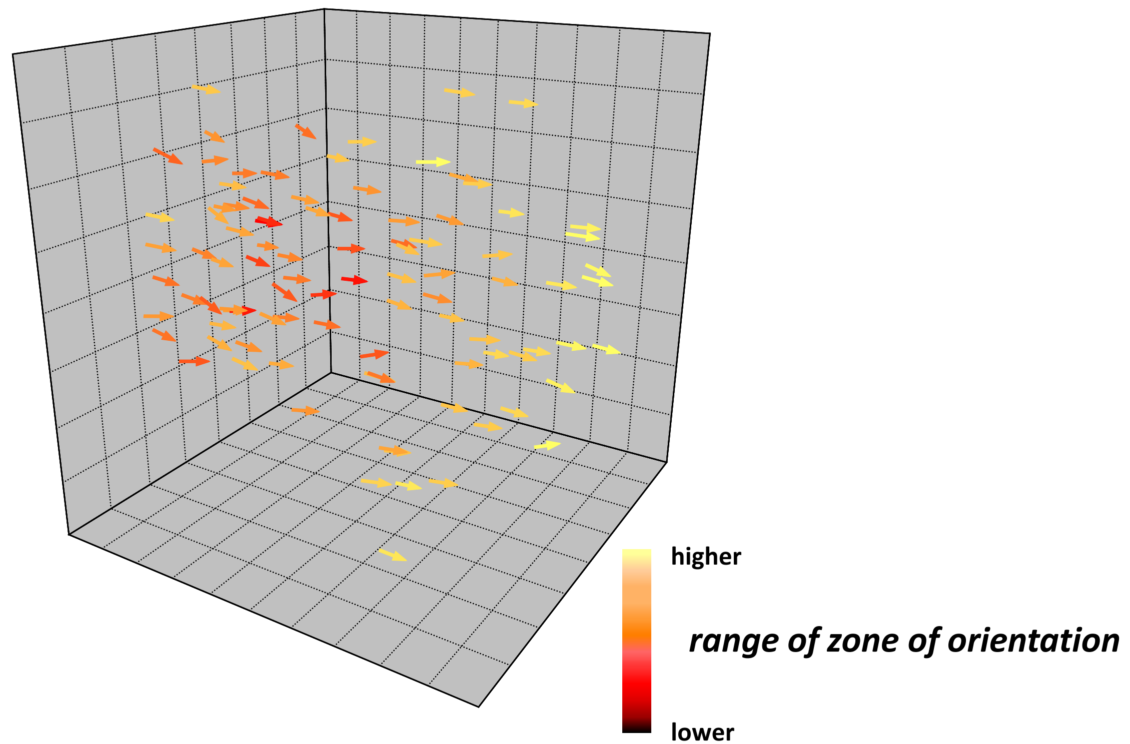


Group motion and collective memory



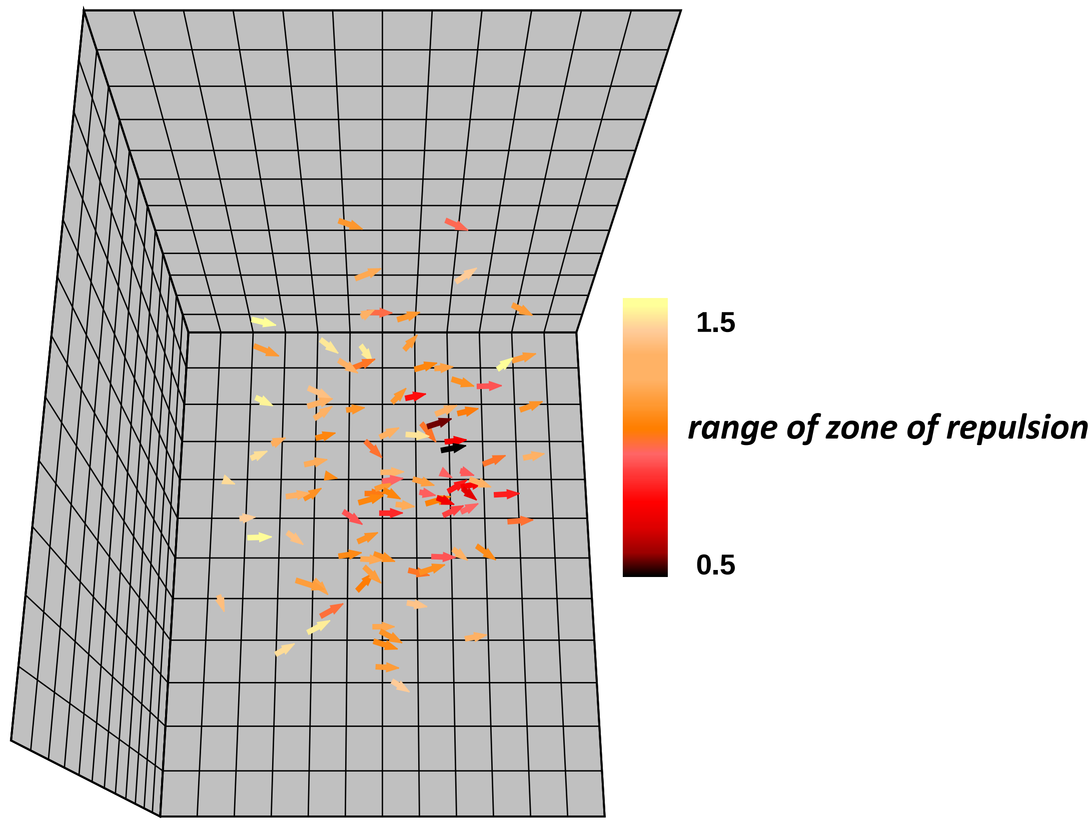


Self-sorting and spatial structure within animal groups

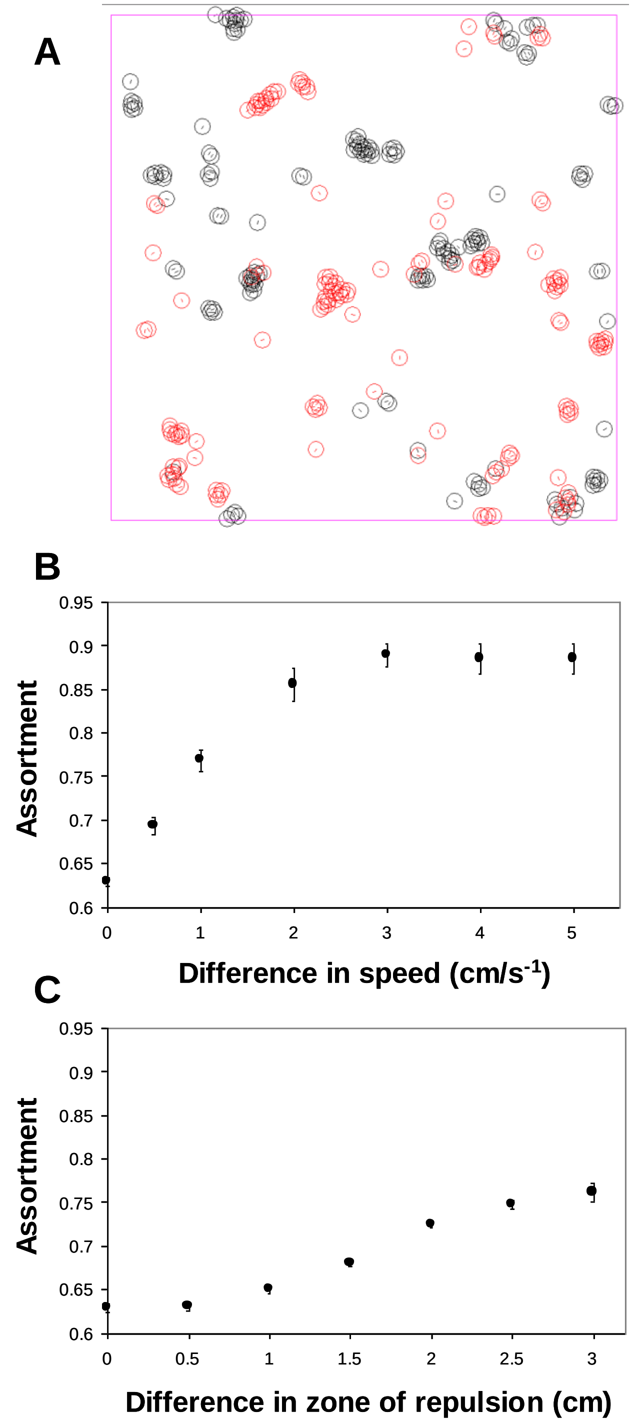


Group motion and collective memory

Self-sorting and spatial structure within animal groups



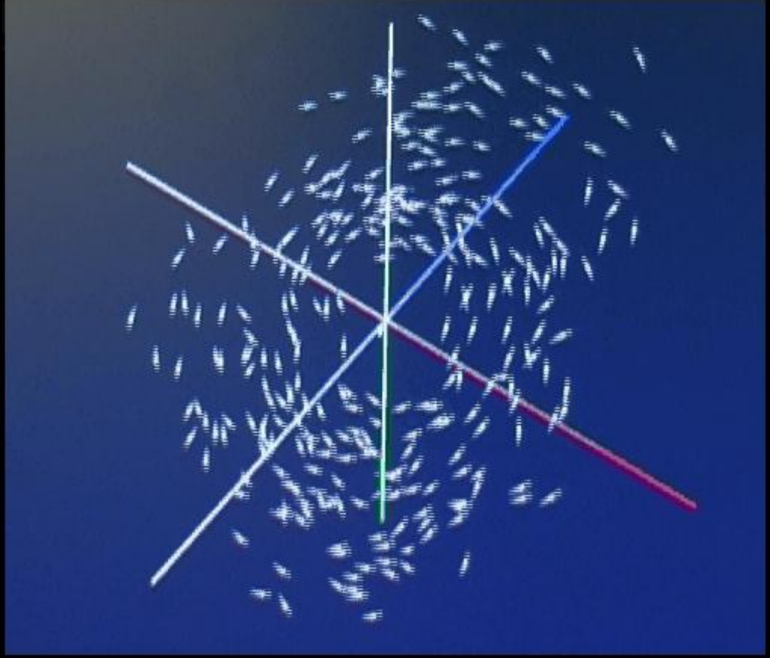
Group motion and collective memory

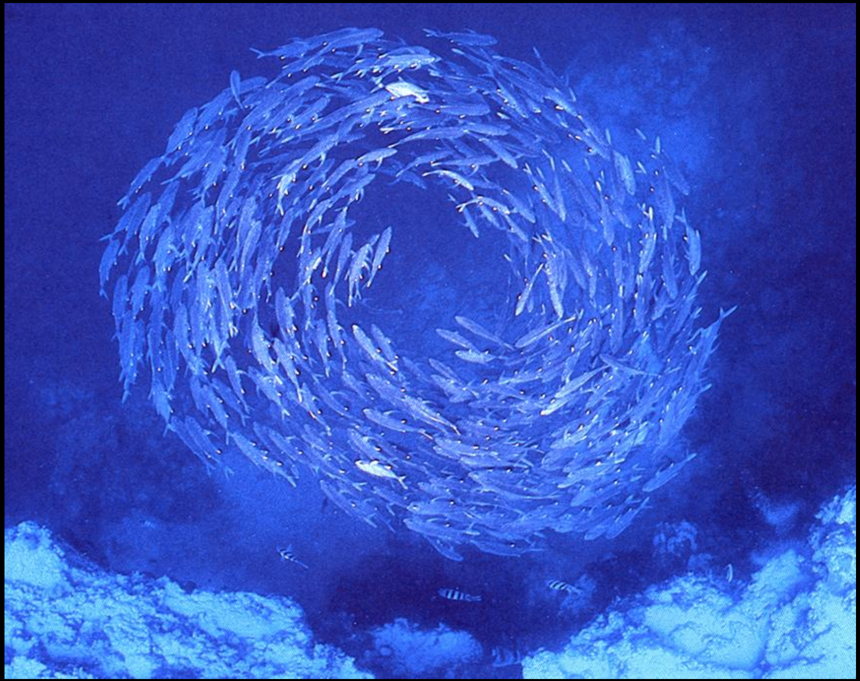


Advances in the Study of Behavior (2003) **32**, 1-75.

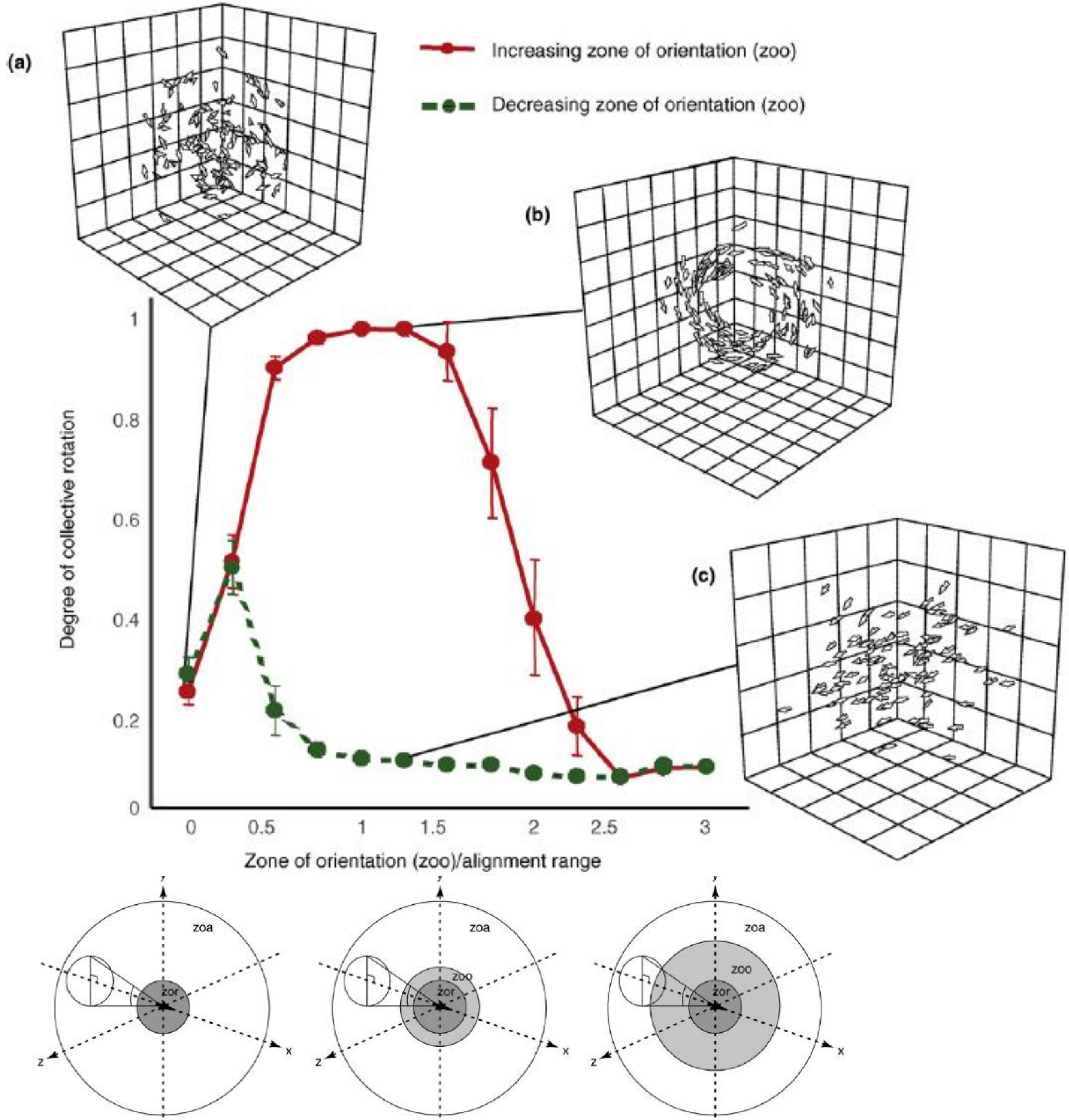
Current Biology (2006) **16**, 169-171

Current Biology (2009)





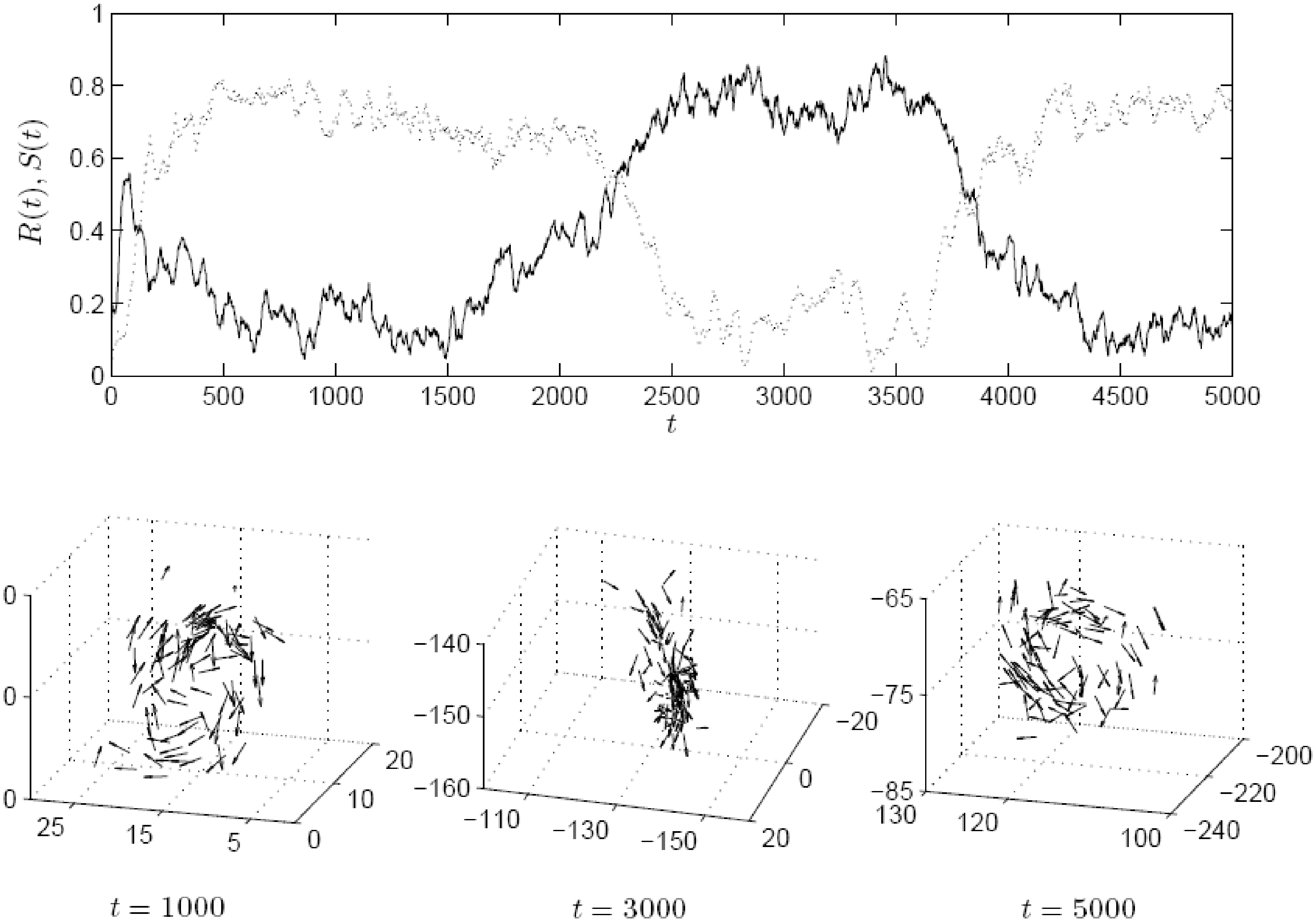
Group motion and collective memory



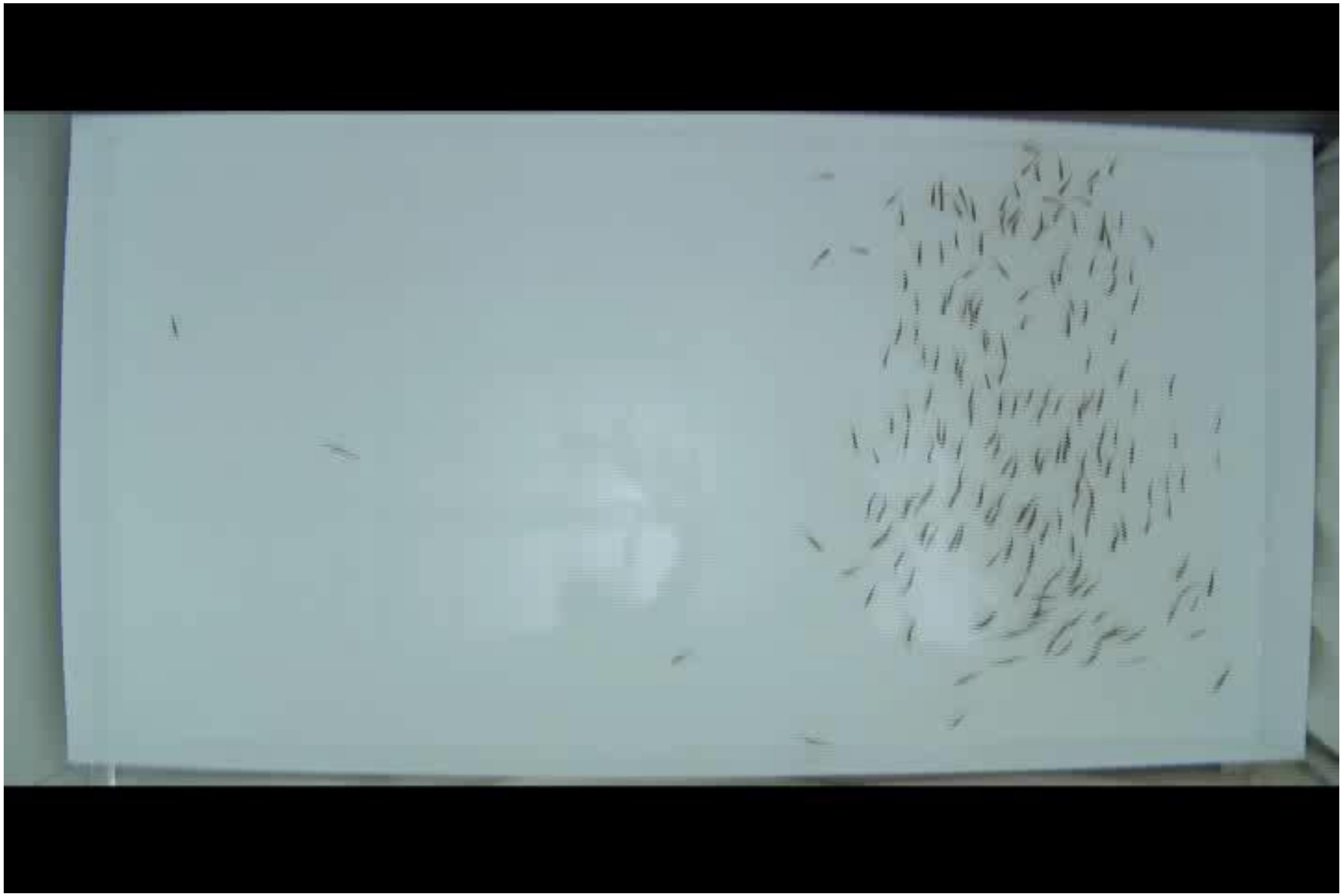
Group motion and collective memory

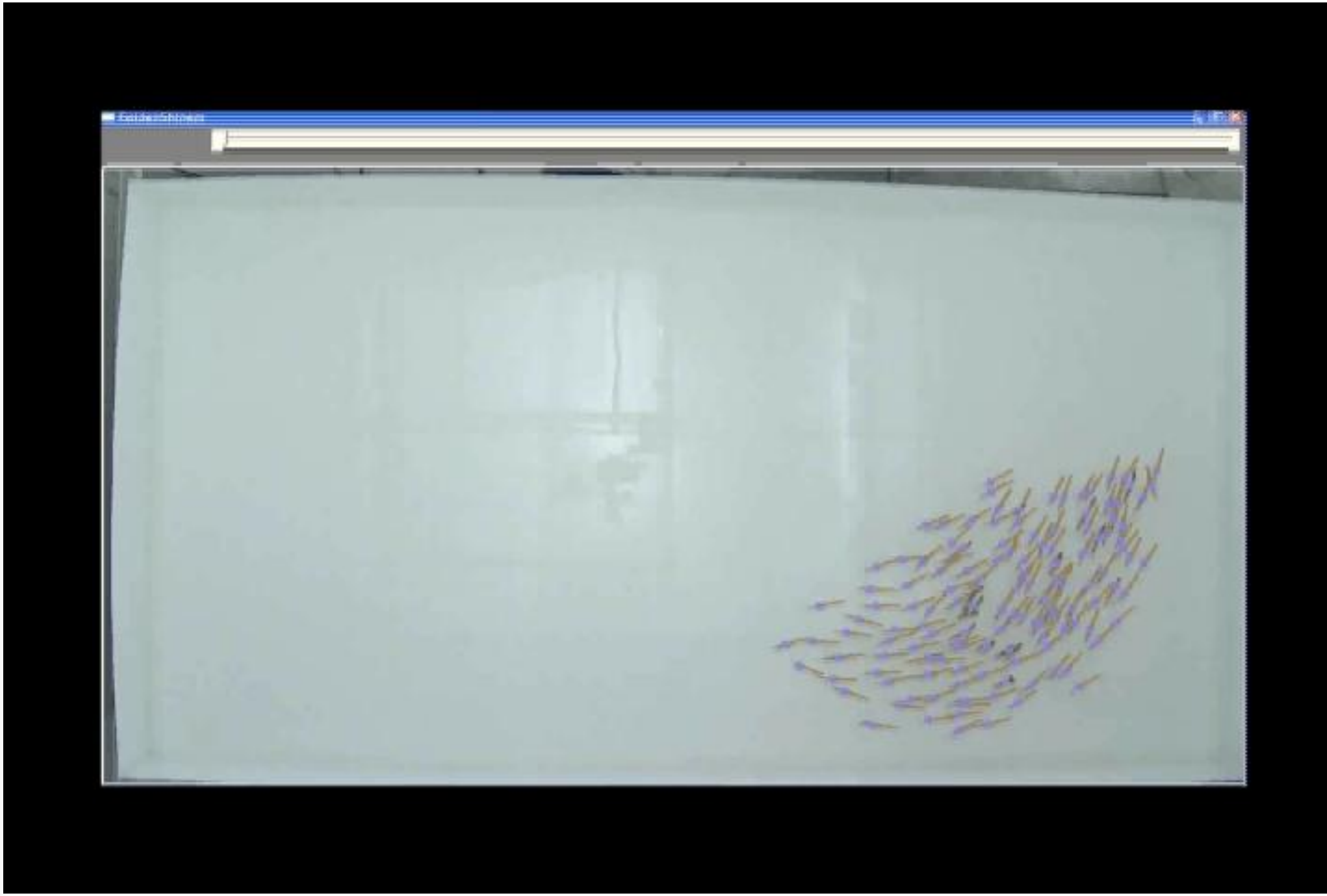
Kolpas et. al. *PNAS* (2007)

Alignment / Polarization = black   Degree of rotation = dotted



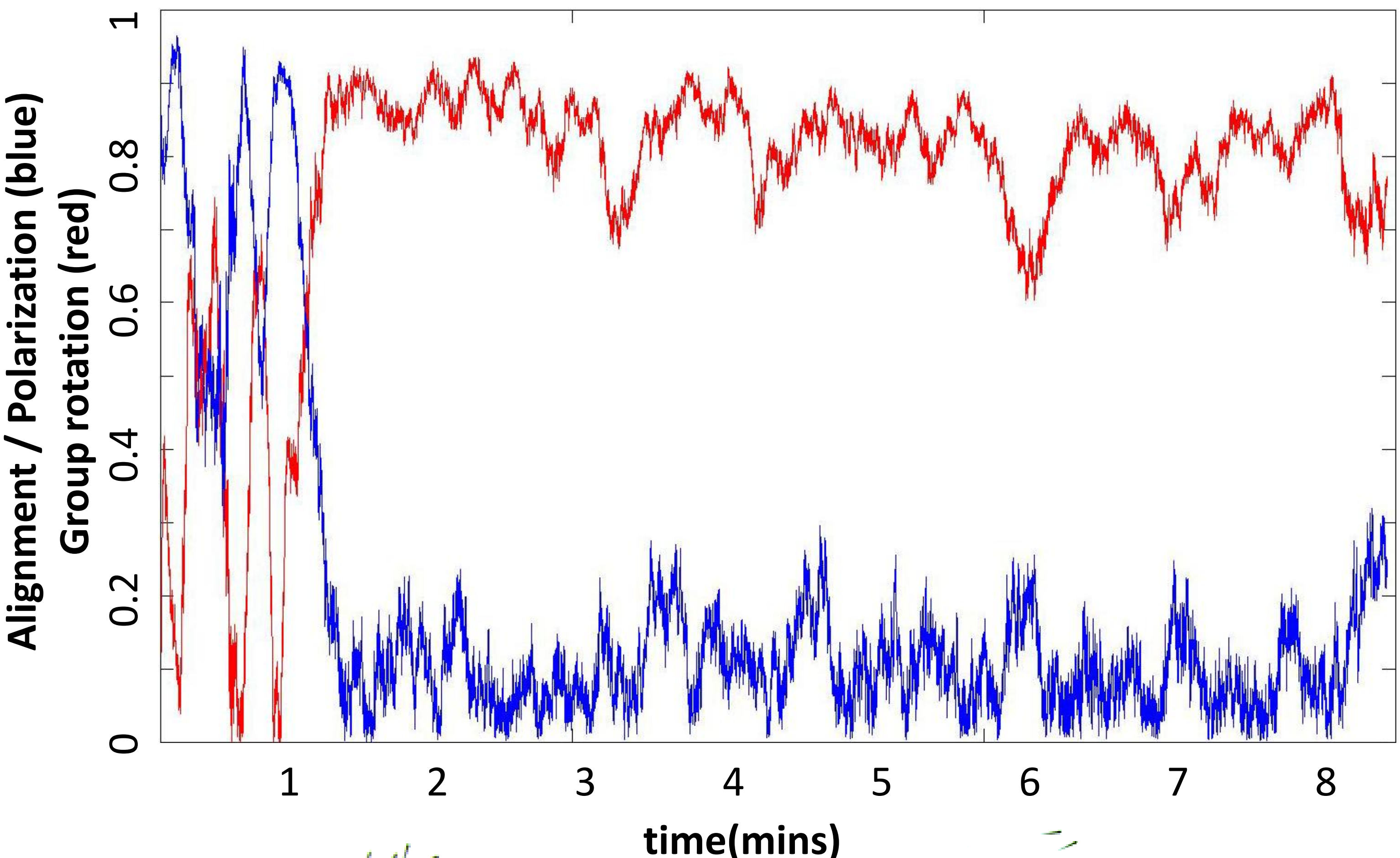
Modeling ⟷ Experiment

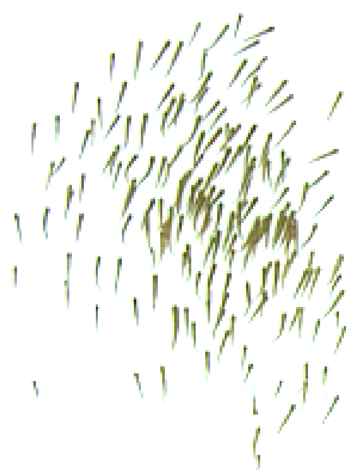




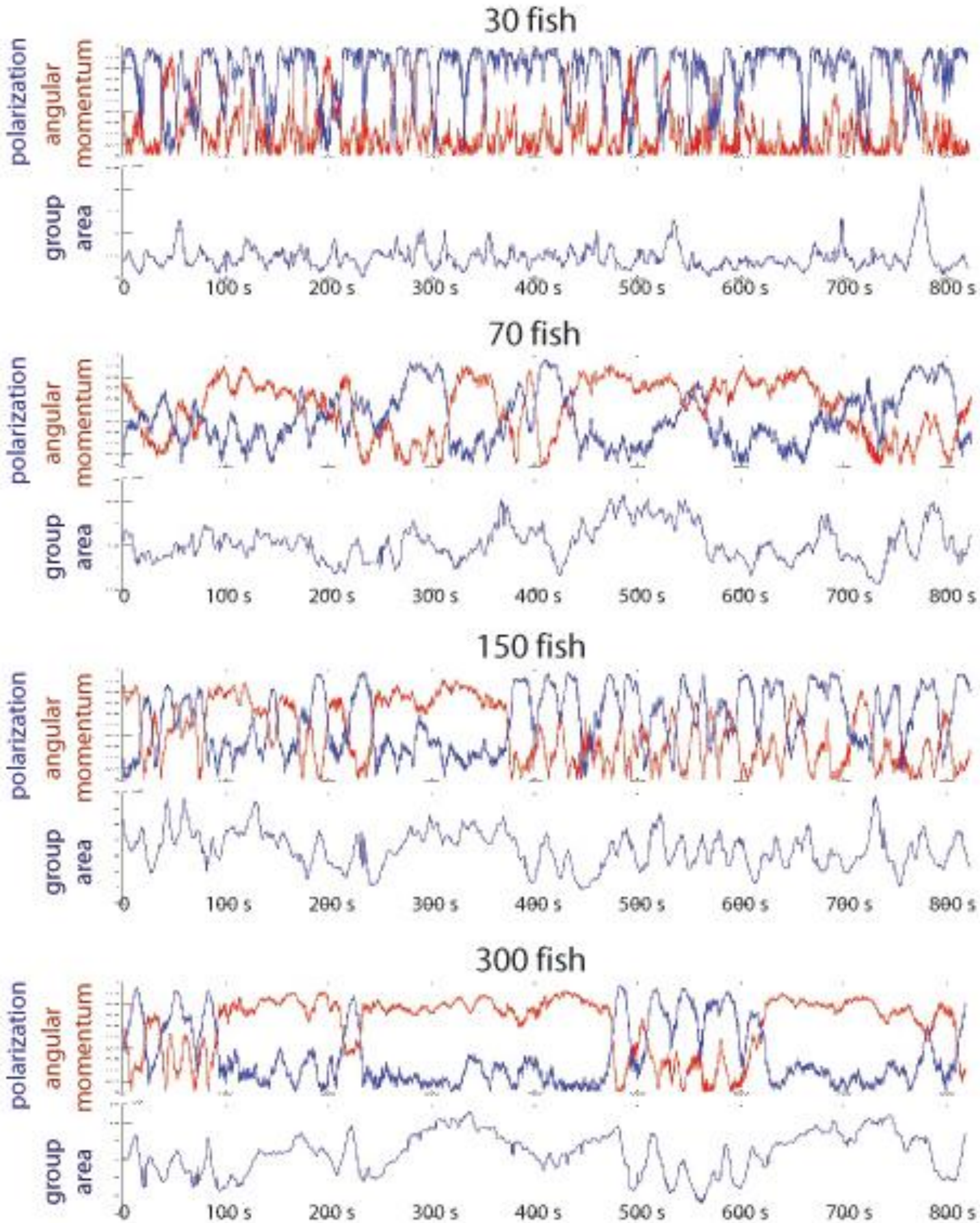
Yael Katz

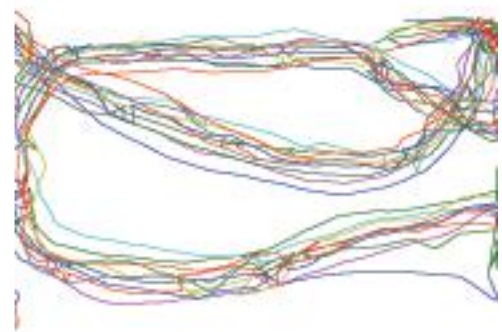
Group motion and collective memory

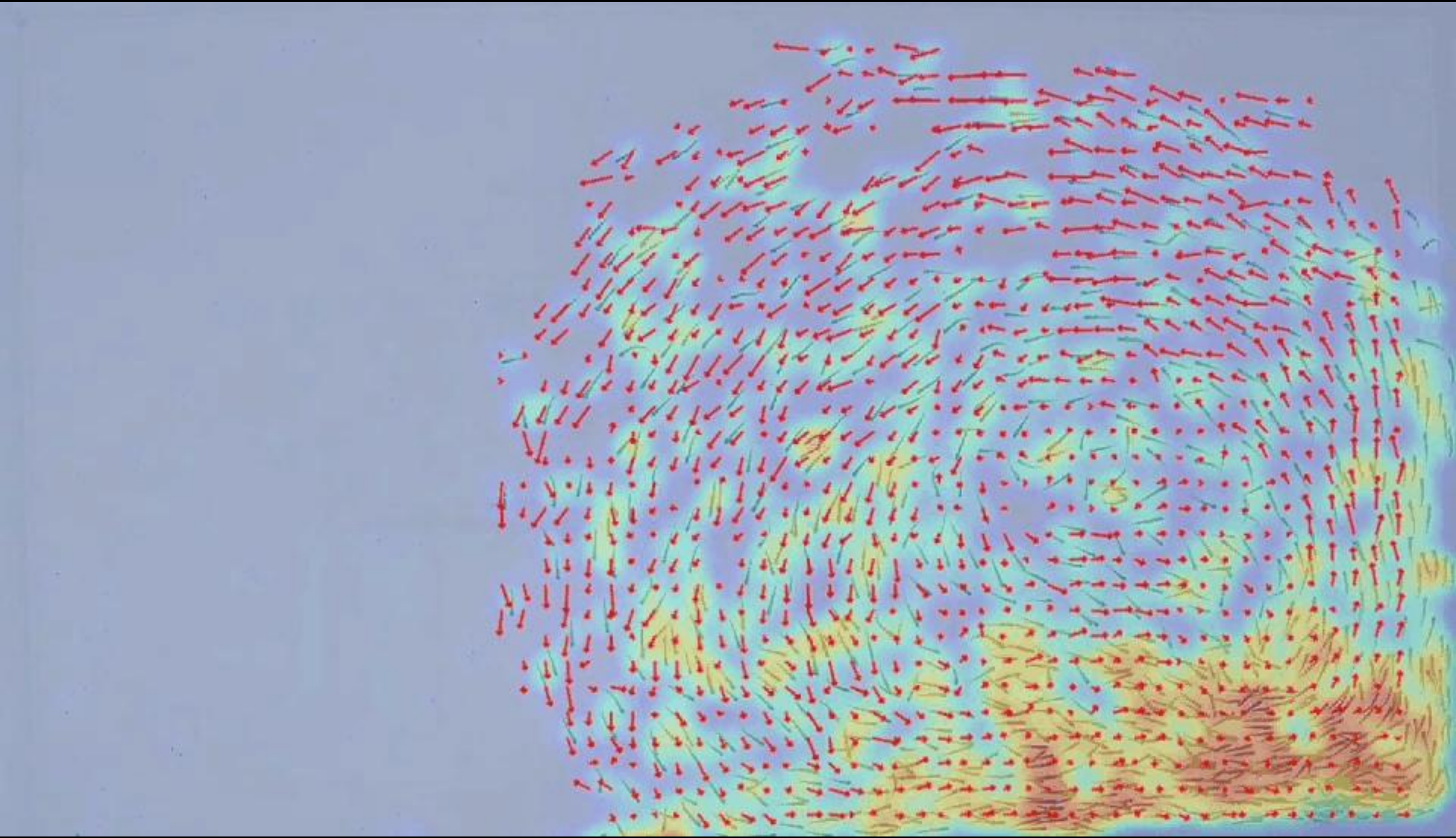




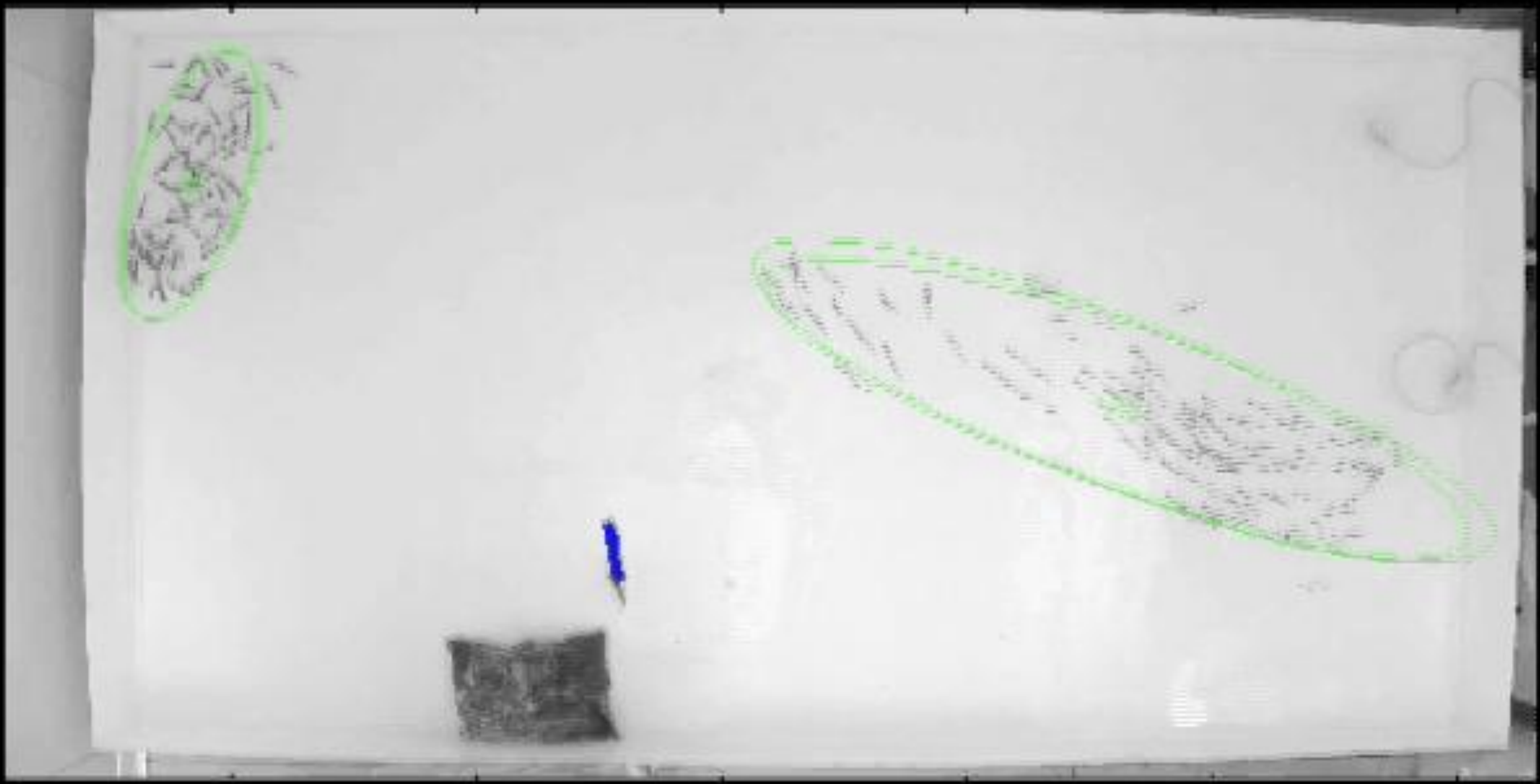
Group motion and collective memory

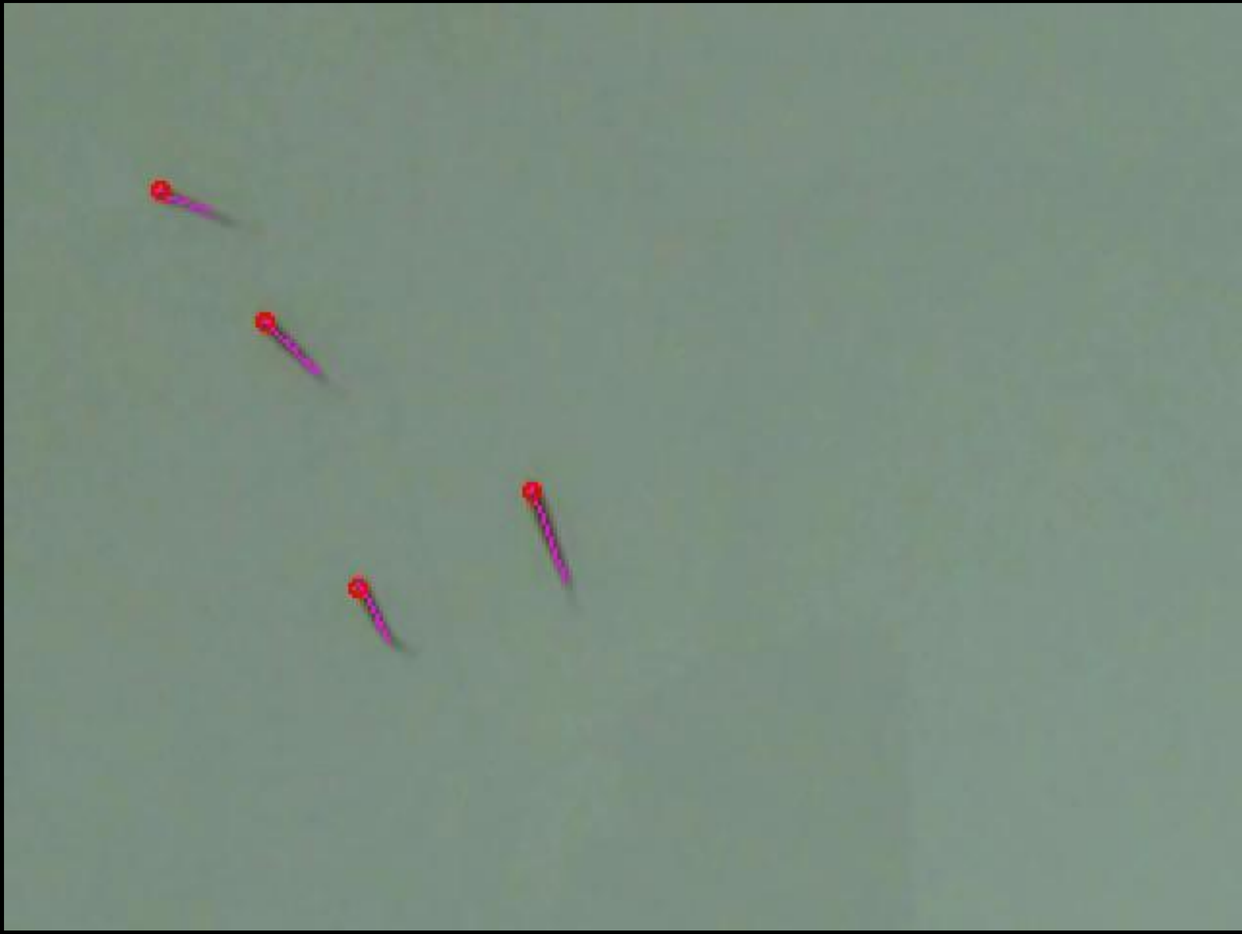


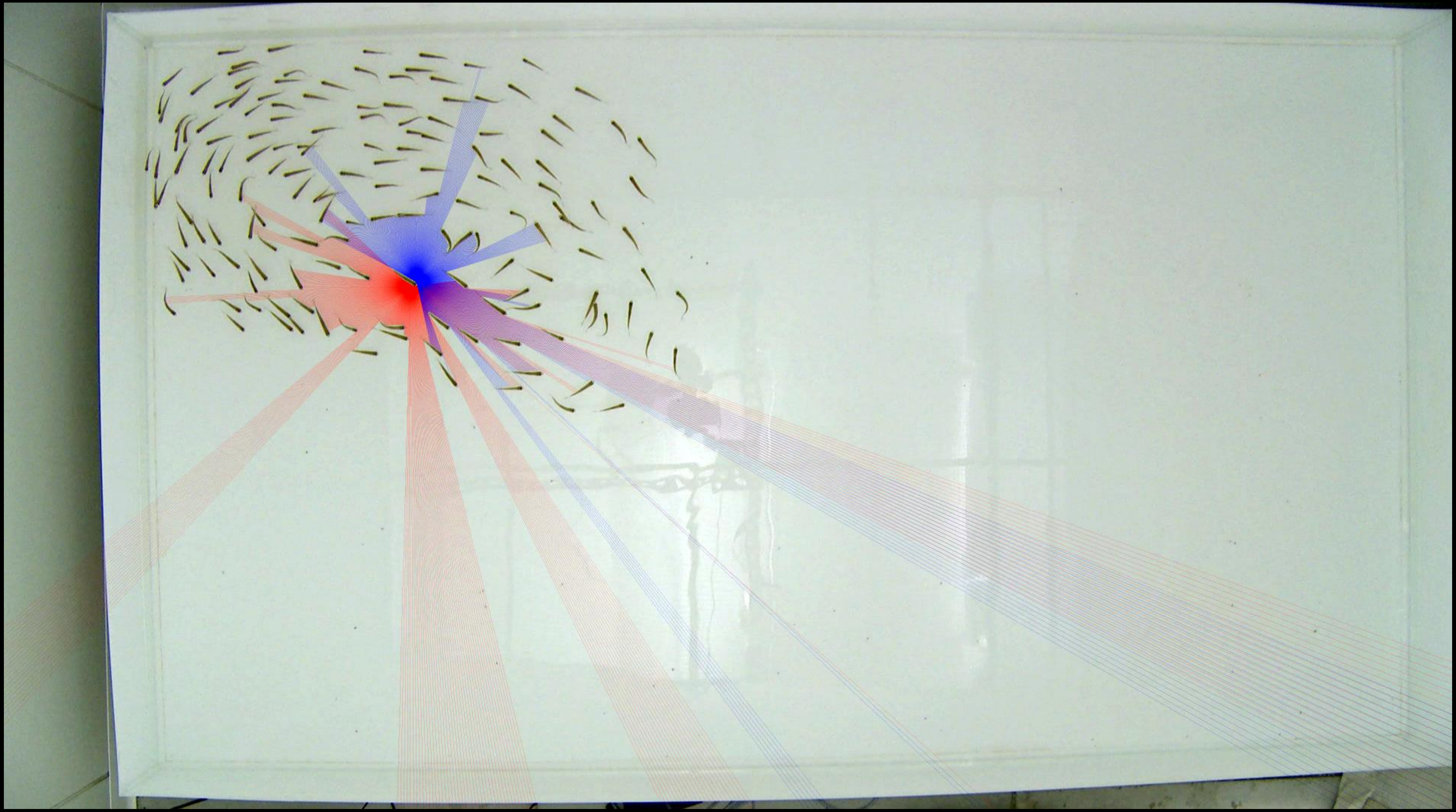




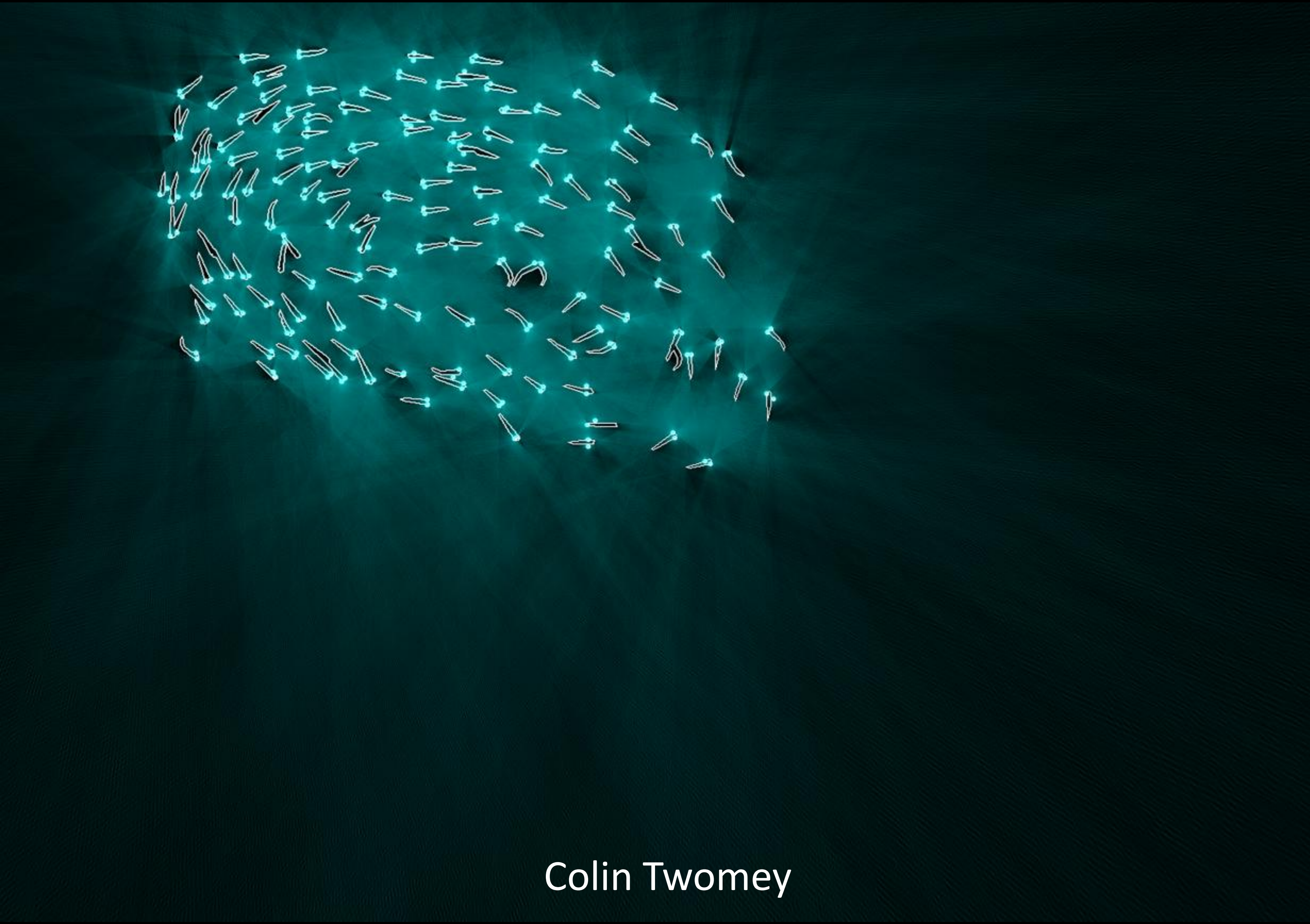
Dan Swain



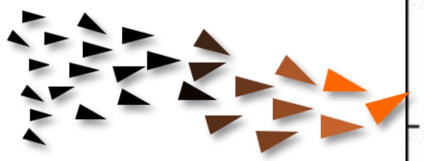




Colin Twomey

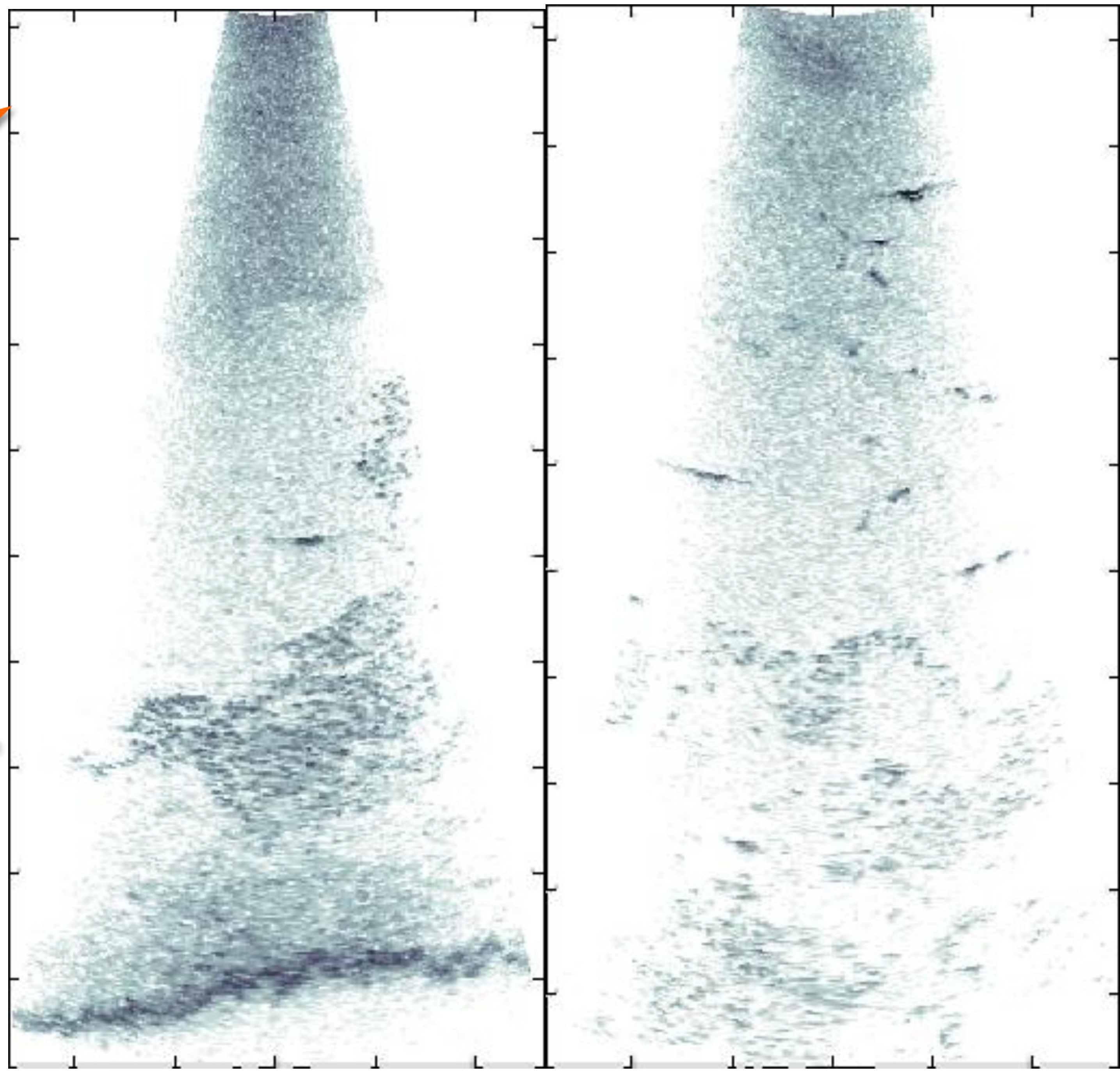


Colin Twomey



Scaling to natural observations and studying group hunting strategies among predators using acoustic cameras

(with Nils Olav Handegard, Kevin Boswell, Simon Leblanc)



NATURE| Vol 445| 15 February 2007

ESSAY

Putting the pieces together

Collective minds

By tapping into social cues, individuals in a group may gain access to higher-order computational capacities that mirror the group's responses to its environment.

Iain Couzin

In 1905 the field naturalist Edmund Selous, a confirmed Darwinian and meticulous observer of bird behaviour, wrote of his wonderment when observing tens of thousands of starlings coming together to roost: "they circle; now dense like a polished roof, now disseminated like the meshes of some vast all-heaven-sweeping net...wheeling, rending, darting…a madness in the sky".

Throughout his life Selous struggled to explain the remarkable synchrony and coherence of motion during flocking, and he concluded that somehow a connectivity of individual minds and transference of thoughts must underlie such behaviour. "They must think collectively, all at the same time, or at least in streaks or patches — a square yard or so of an idea, a flash out of so many brains".

We now know that such synchronized group behaviour is mediated detected by only a relatively small proportion of group members due to limitations in individual sensory capabilities, often further restricted by crowding. Close behavioural coupling among near neighbours, however, allows a localized change in direction to be amplified, creating a rapidly growing and propagating wave of turning across the group. This positive feedback results from the ability of indi-

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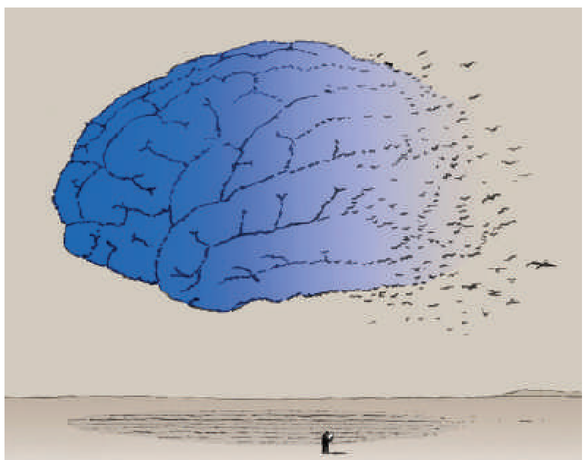


Couzin, *Nature* (2007)

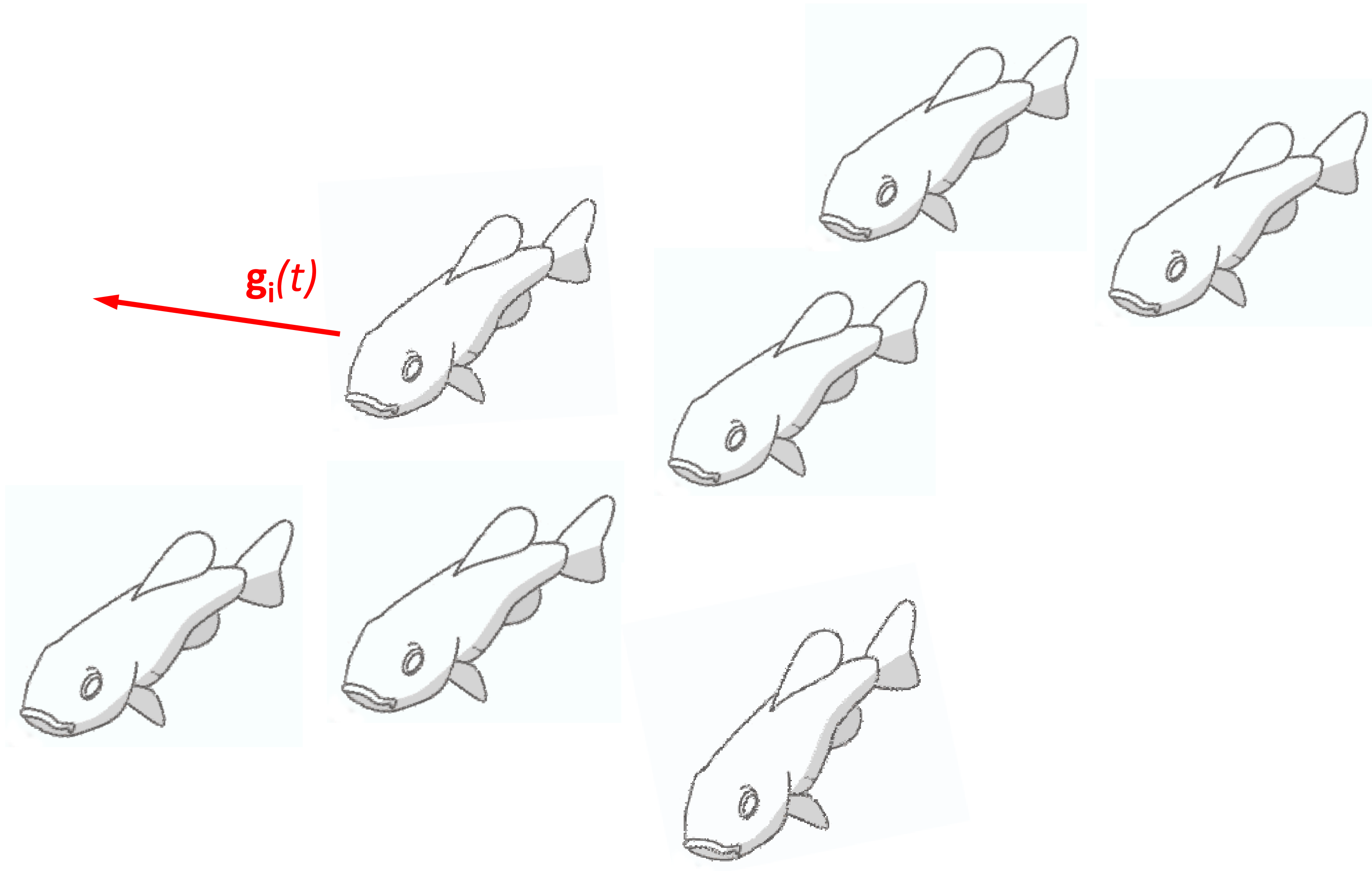
Couzin, *TICS* (2009)

Leadership and collective decision-making

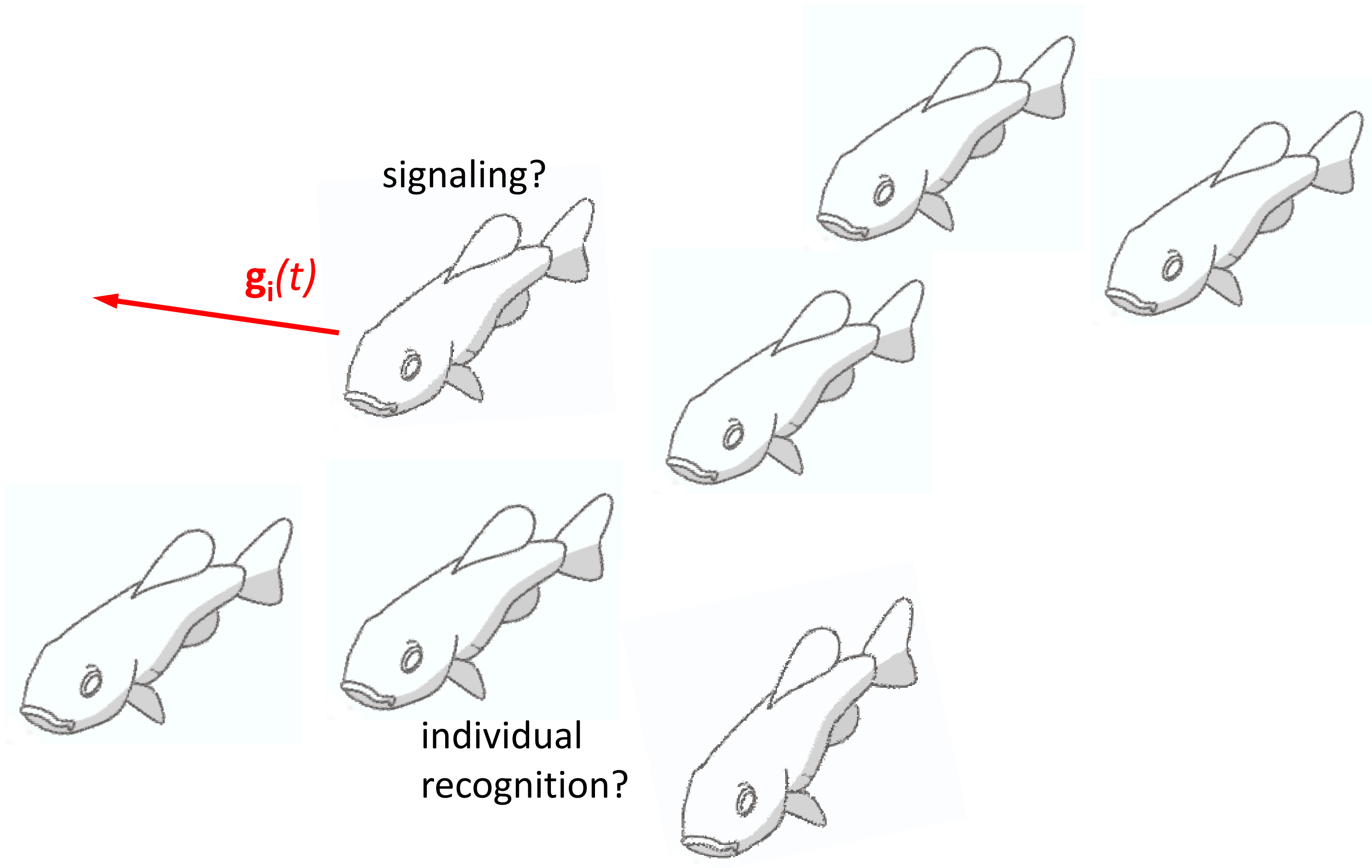
How do grouping animals make informed unanimous decisions?

Couzin *et al. Nature* (2005) **433**, 513-516

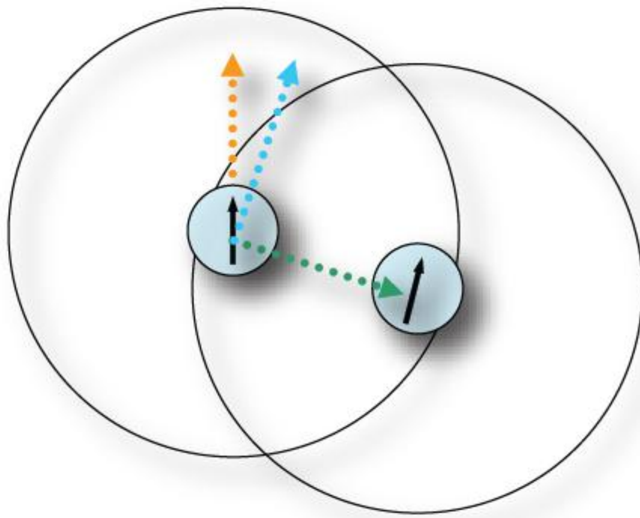
Collective decision-making



Collective decision-making



Social interactions

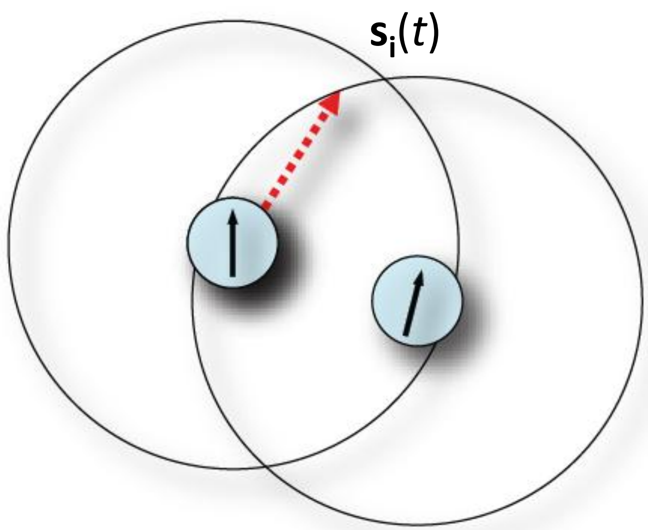


Attraction Alignment

$$\mathbf{d}_i(t+\Delta t) = \sum_{j\neq i} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{|(\mathbf{c}_j(t) - \mathbf{c}_i(t))|} + \sum_{j=1} \frac{\mathbf{v}_j(t)}{|\mathbf{v}_j(t)|}$$

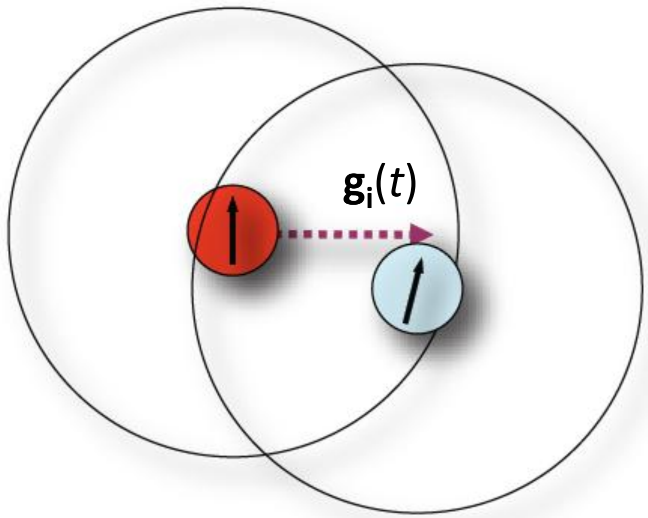
Collective decision-making

Social interactions



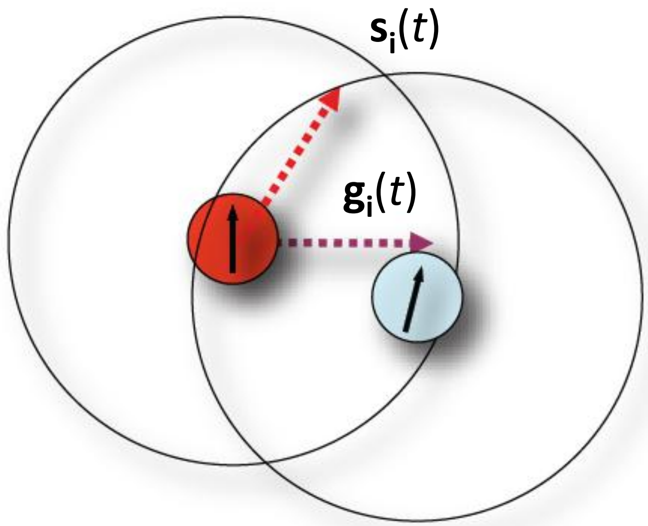
Collective decision-making

Informed individuals



Collective decision-making

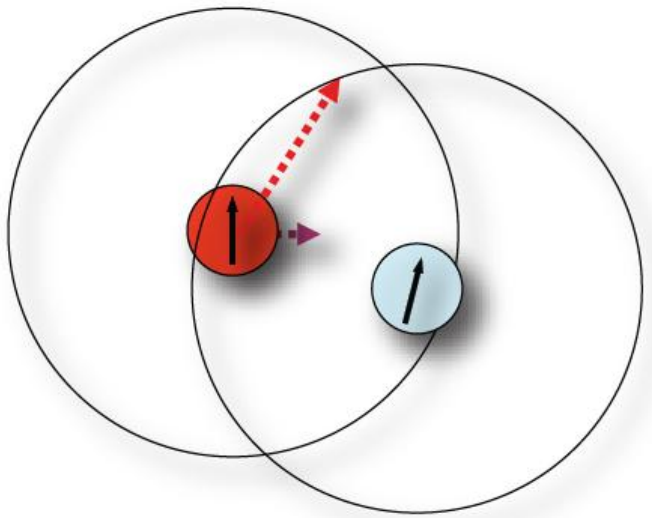
Informed individuals



$$\mathbf{d}_i(t+\Delta t) = \frac{\mathbf{s}_i(t) + \omega\, \mathrm{g}_i(t)}{|\, \mathbf{s}_i(t) + \omega\, \mathrm{g}_i(t) \,|}$$

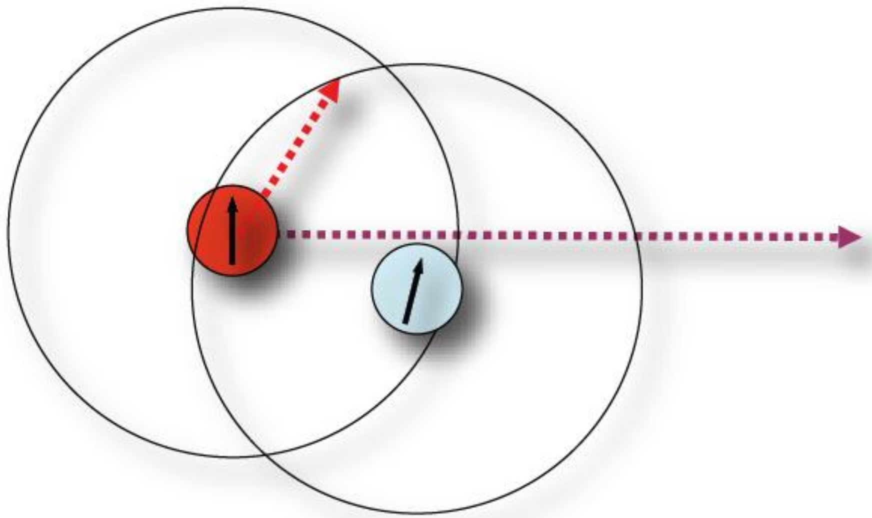
Collective decision-making

Low ω – weak directional preference



$$\mathbf{d}_i(t+\Delta t) = \frac{\mathbf{s}_i(t) + \omega\, \mathrm{g}_i(t)}{|\, \mathbf{s}_i(t) + \omega\, \mathrm{g}_i(t)\, |}$$

High ω – strong directional preference



$$\mathbf{d}_i(t+\Delta t) = \frac{\mathbf{s}_i(t) + \omega\, g_i(t)}{|\, \mathbf{s}_i(t) + \omega\, g_i(t) \,|}$$

Collective decision-making

1 informed individual in group of 100

Collective decision-making

preferred direction

5 informed individuals in group of 100

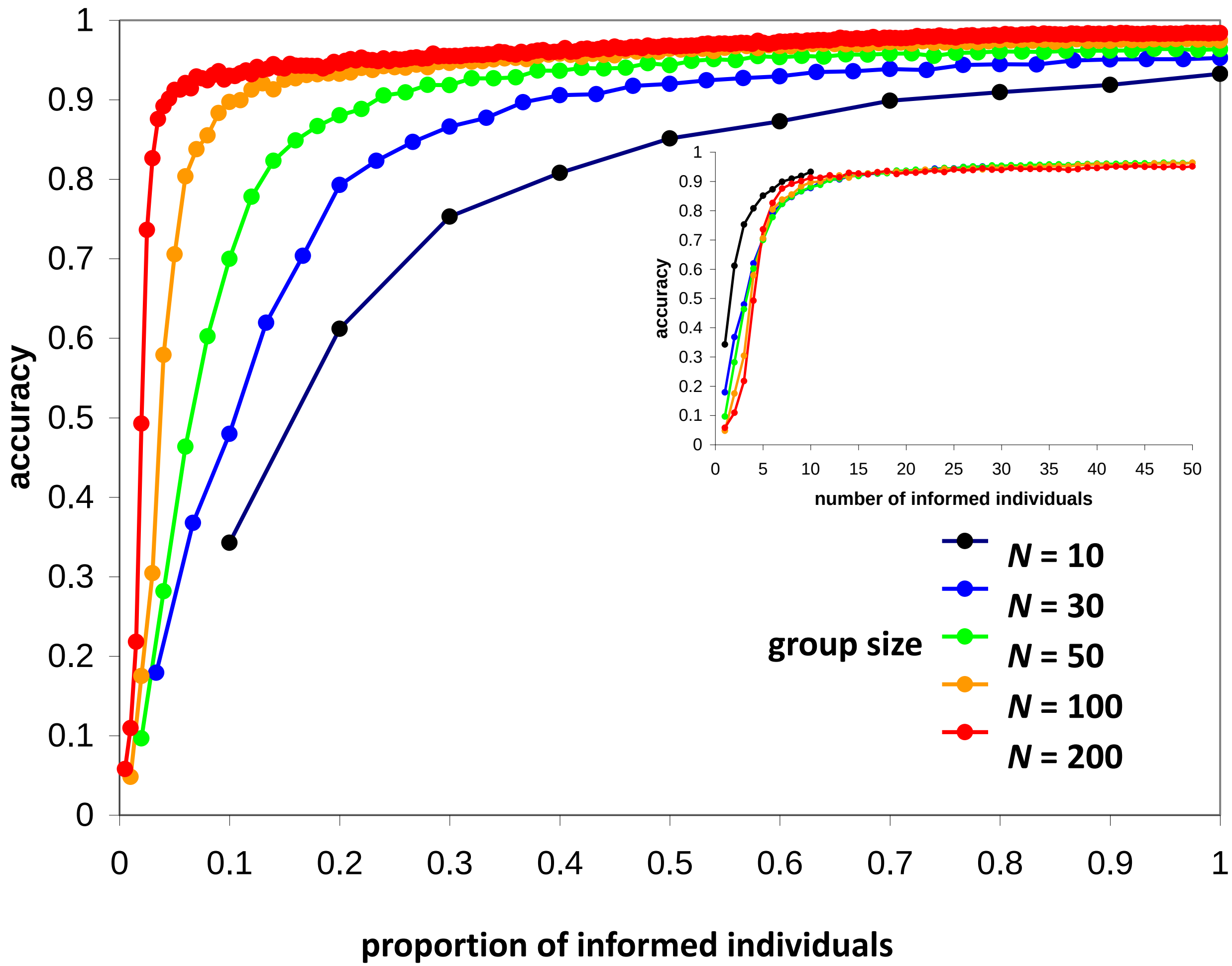
Collective decision-making

preferred direction

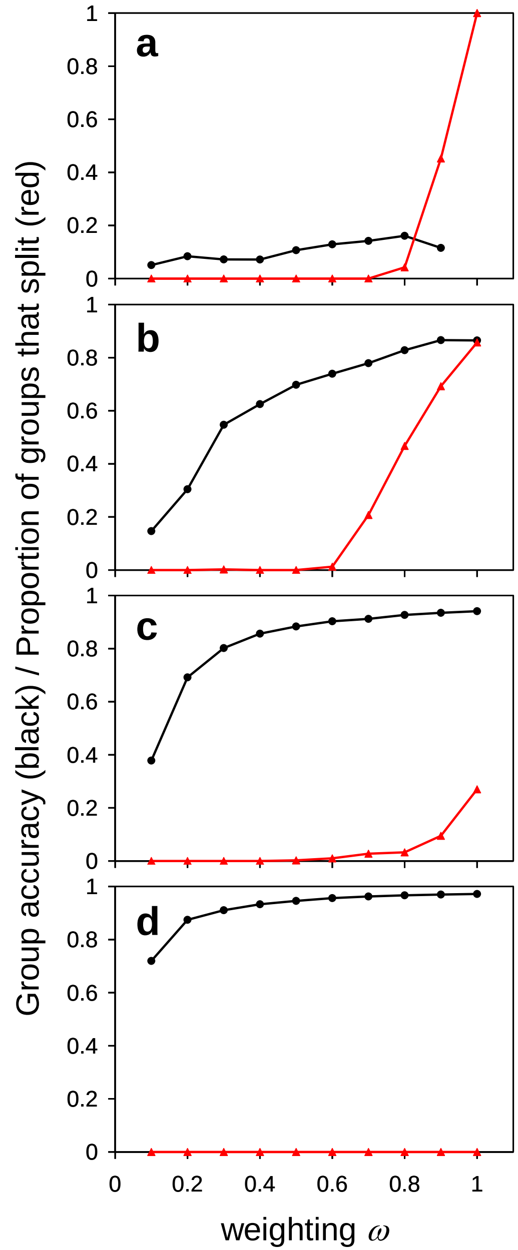
10 informed individuals in group of 100

Collective decision-making

The subtle guide hypothesis



Collective decision-making



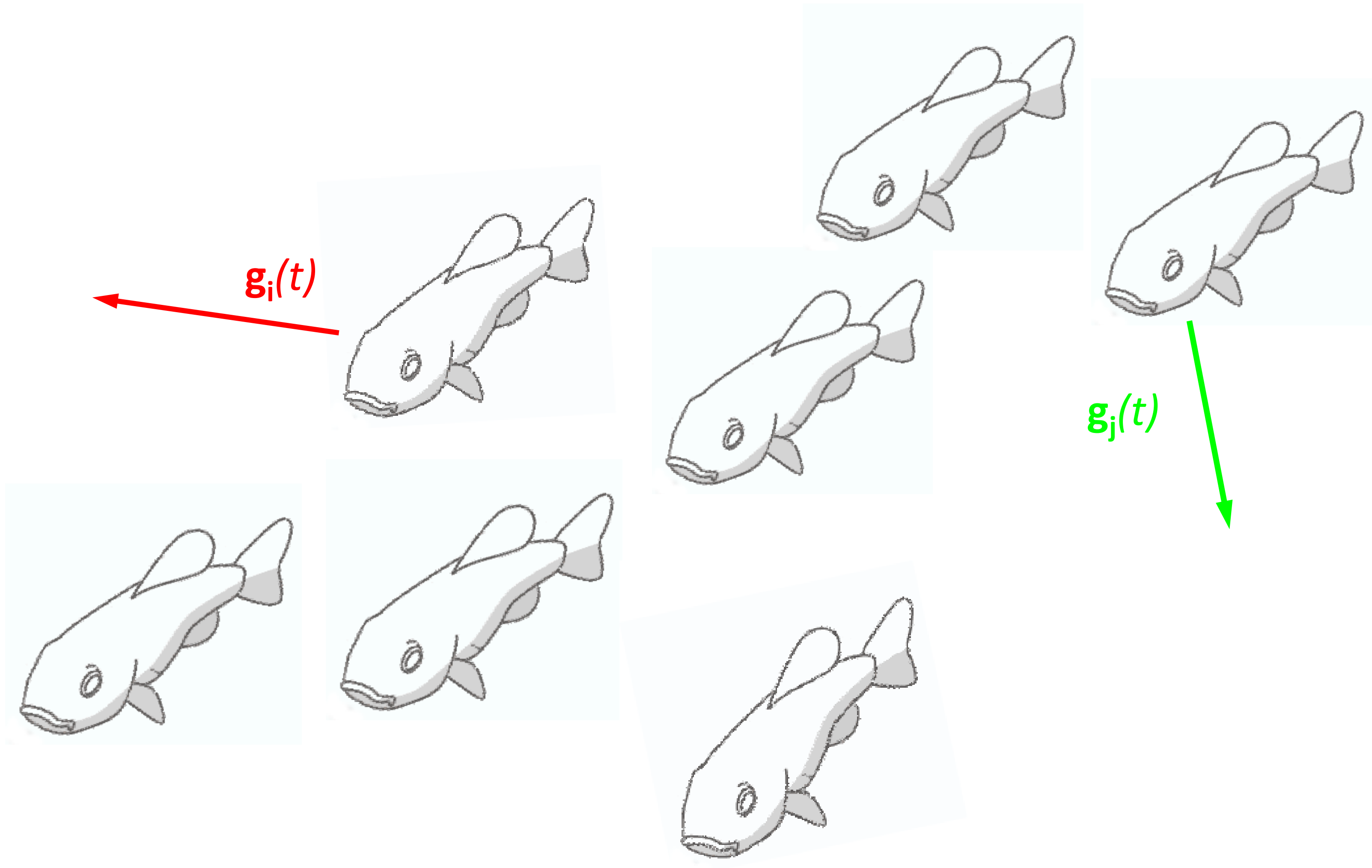
Increasing number of informed individuals

Differences in experience or motivation

Differences in experience or motivation

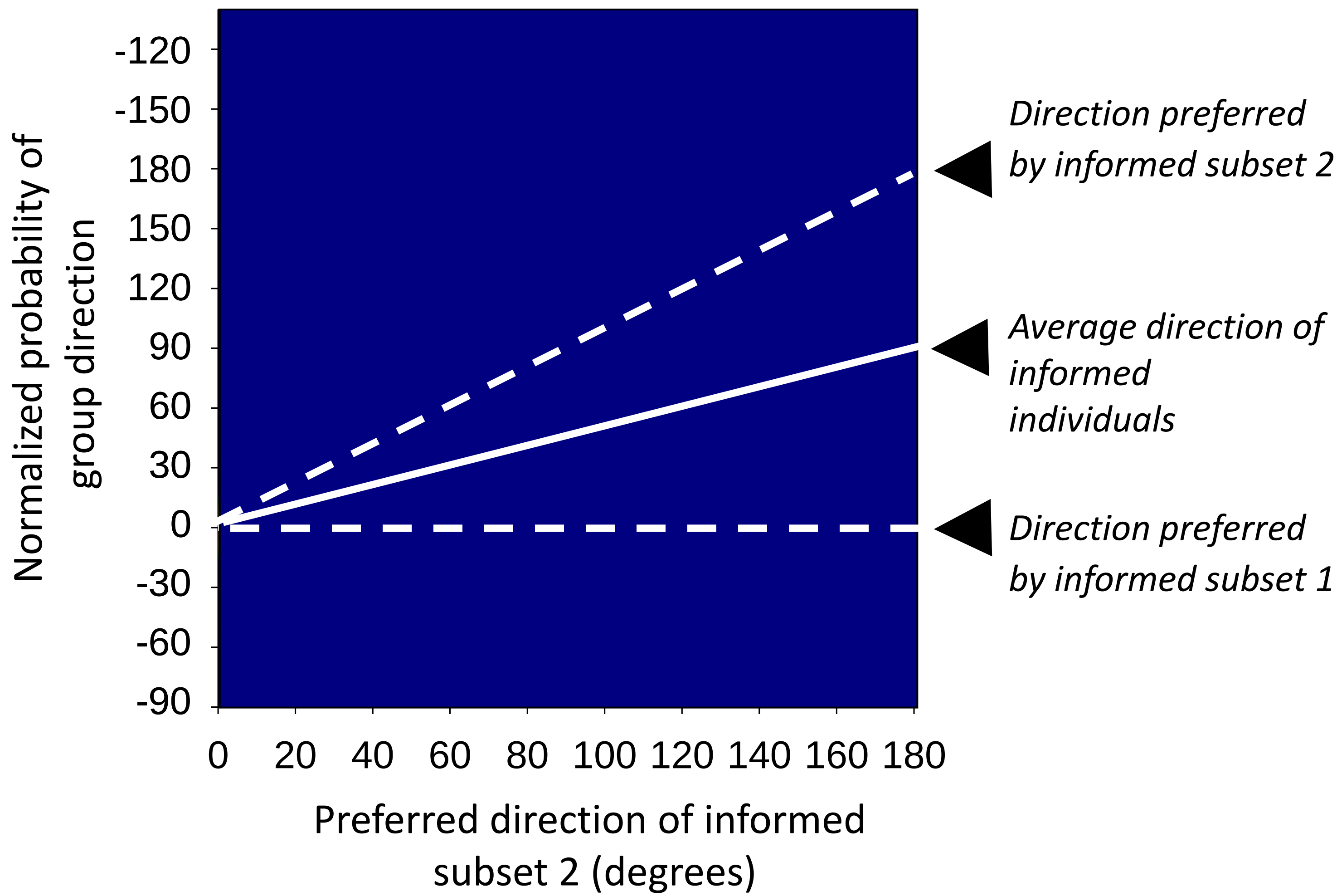
Collective consensus decisions

Collective decision-making



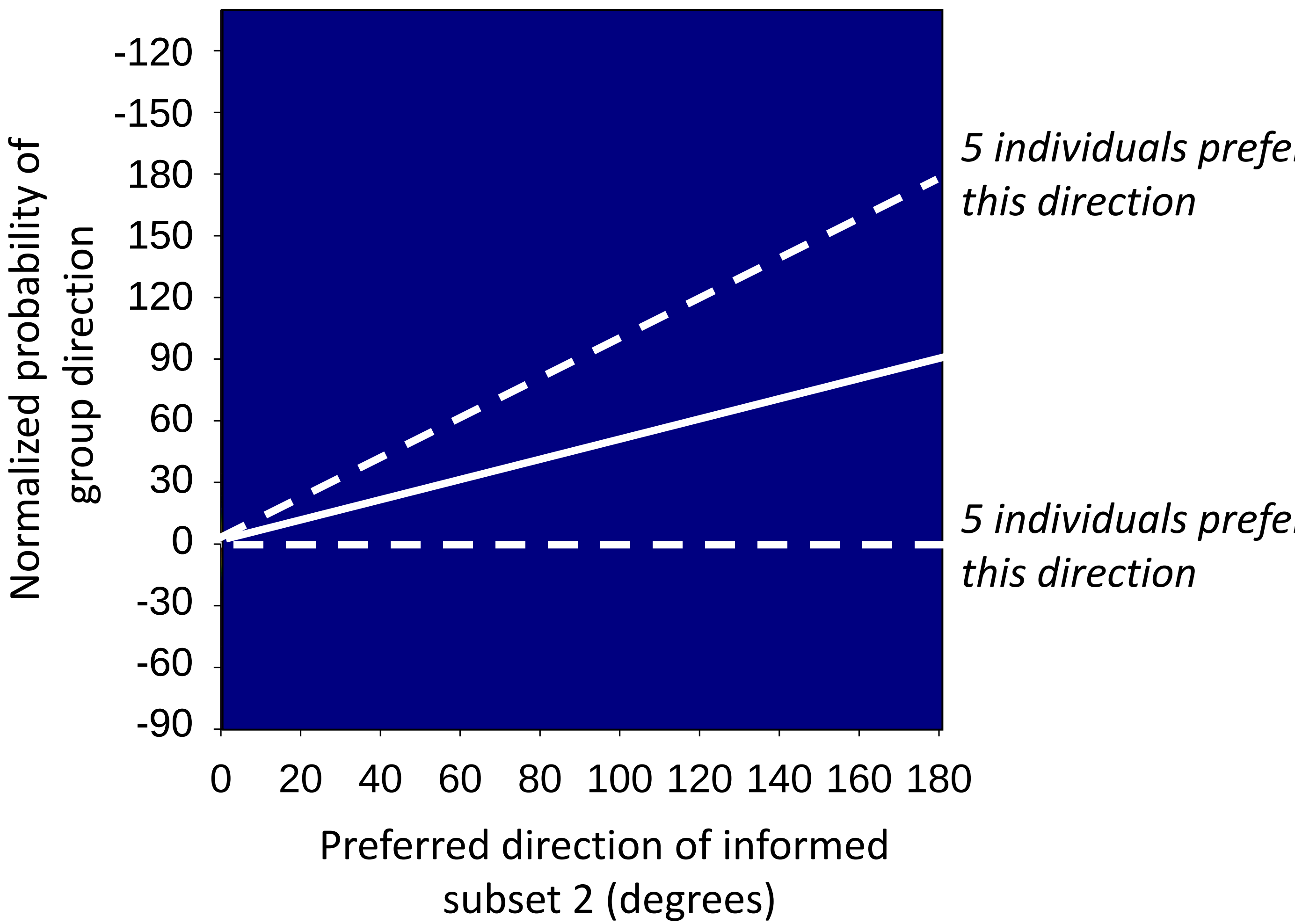
Collective decision-making

Equal number of individuals with opposing preferences



Equal number of individuals with opposing preferences

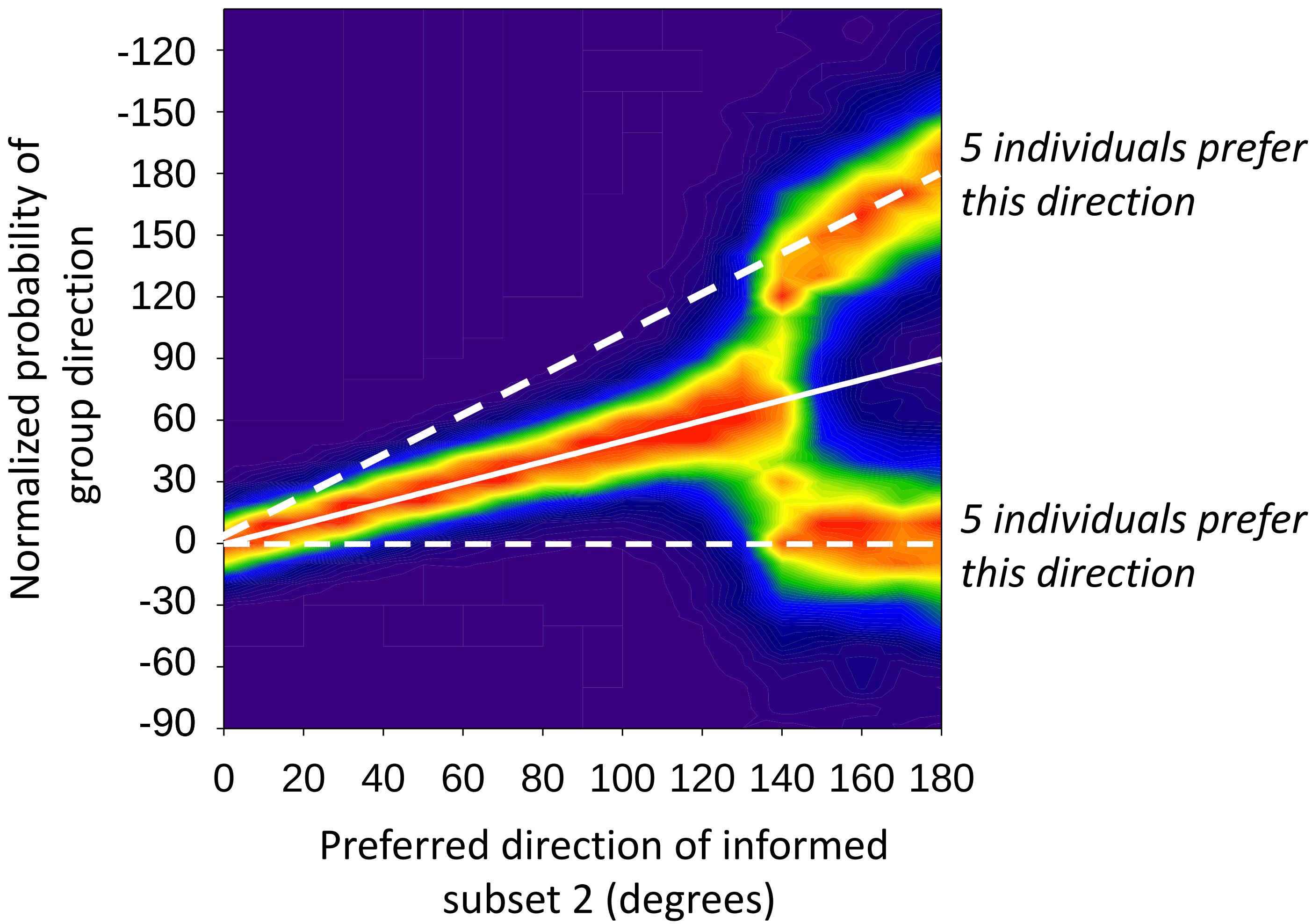
Total group size = 100



Collective decision-making

Equal number of individuals with opposing preferences

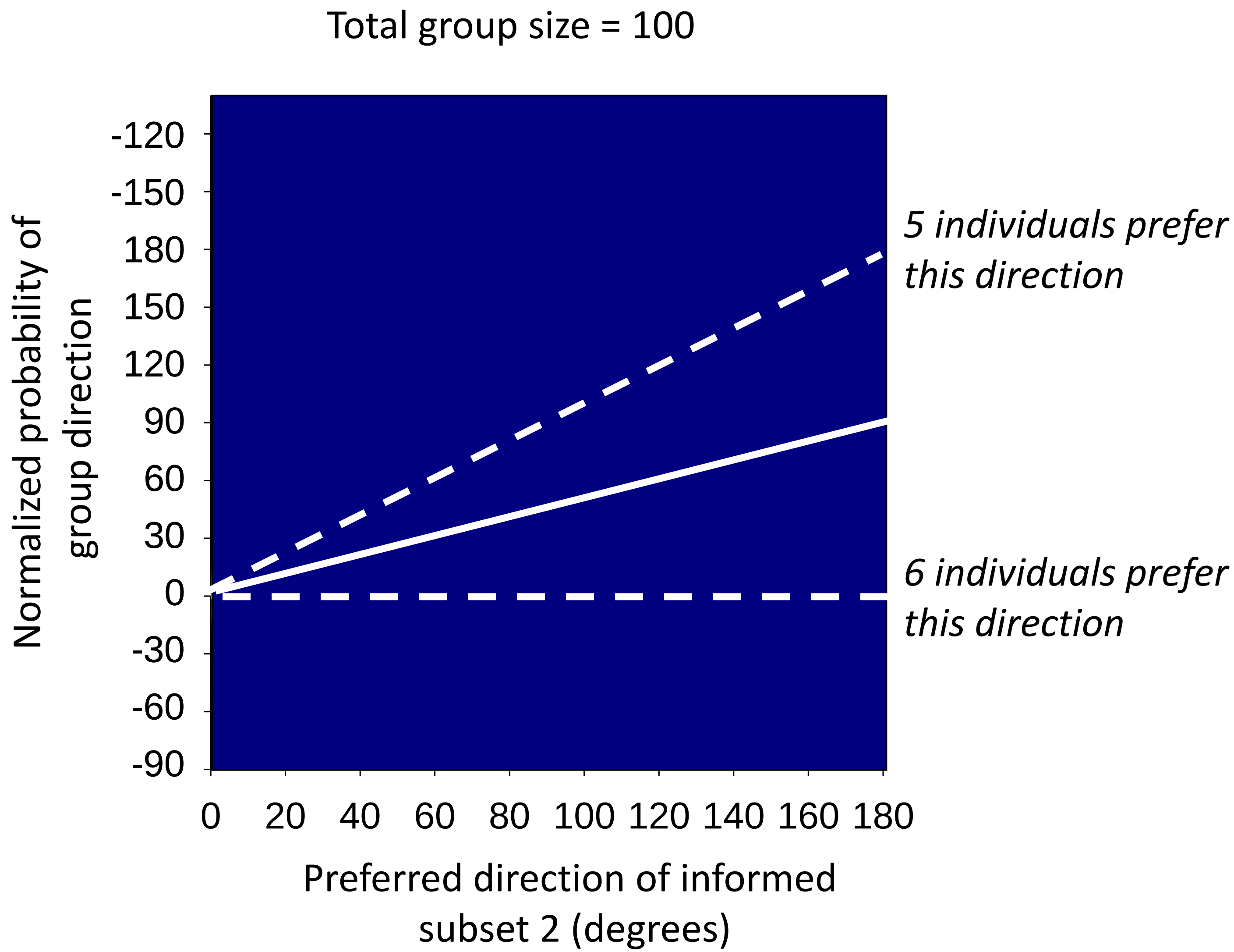
Total group size = 100



Unequal number of individuals with opposing preferences

Add 1 extra individual to one of the informed groups
(1% of total group size)

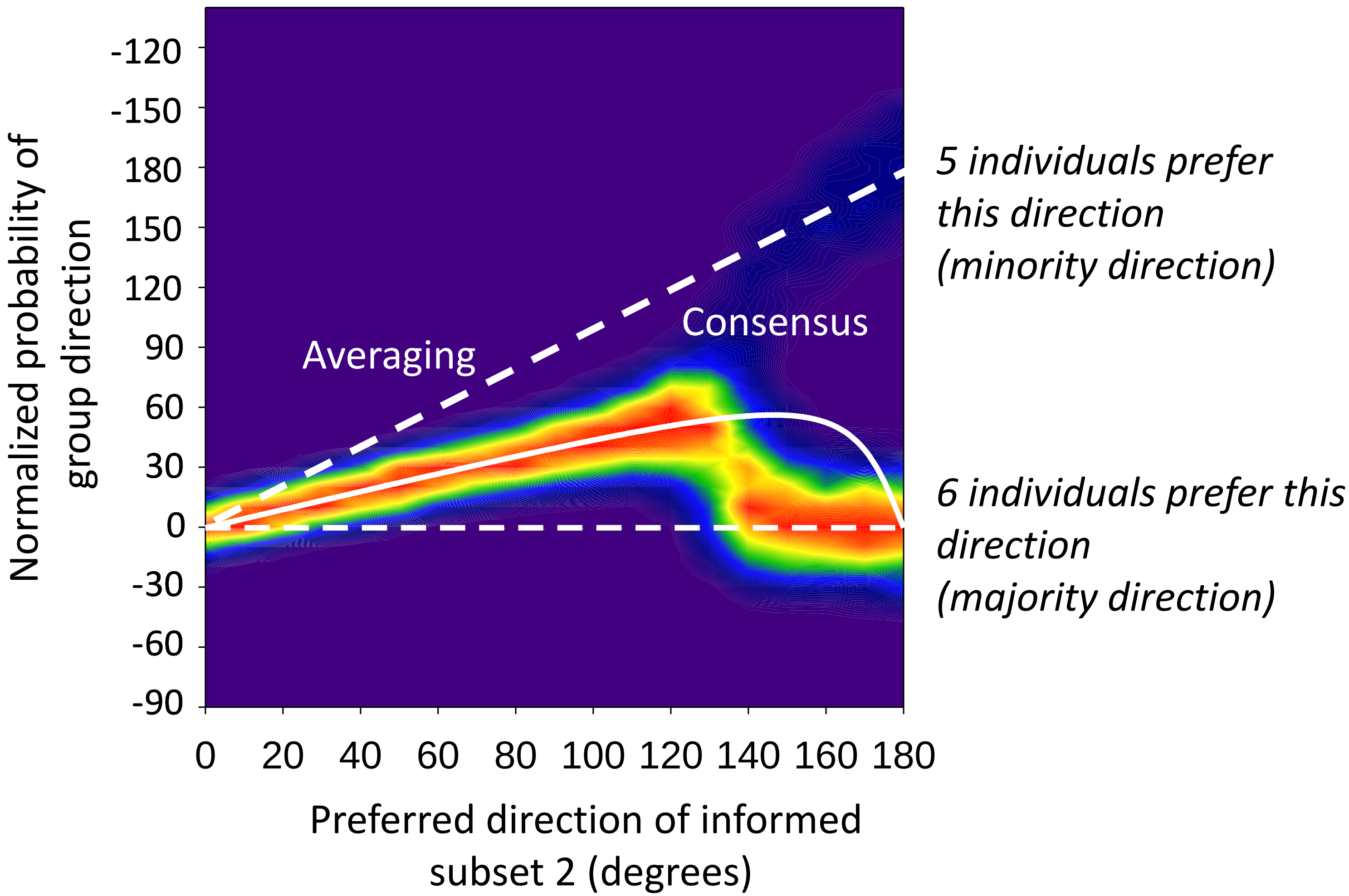
Equal number of individuals with opposing preferences



Collective decision-making

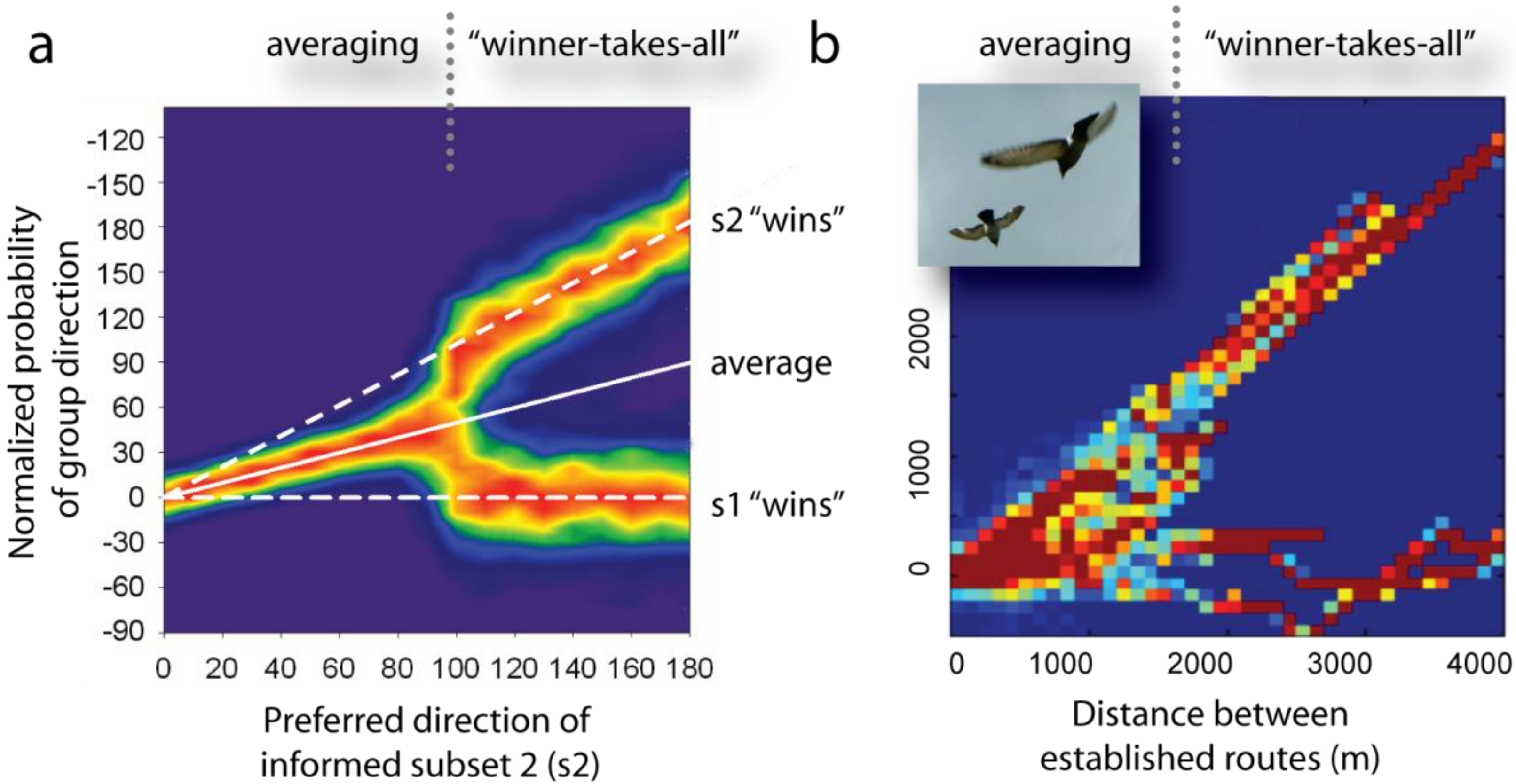
Unequal number of individuals with opposing preferences

Total group size = 100



Collective decision-making

Biro *et al*, (2006)



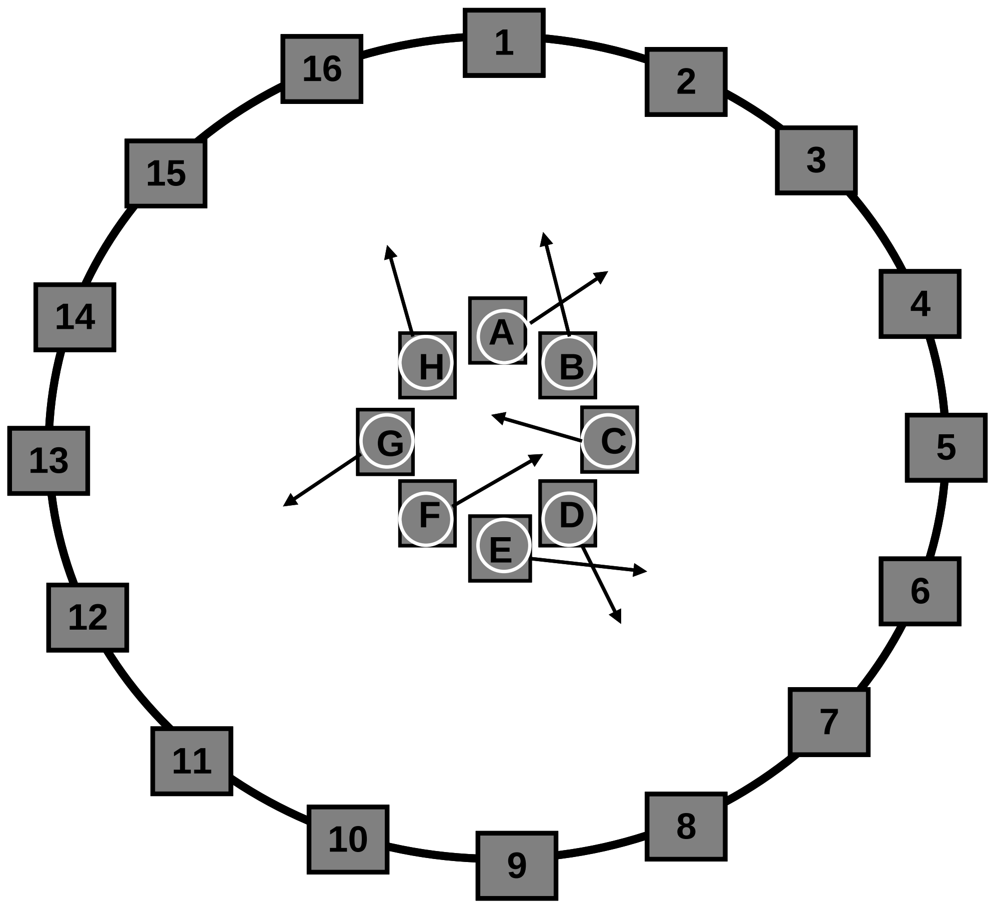
Collective decision-making

Humans

Animal Behaviour (2008)

Phil. Trans. Roy. Soc. Lond. B. (2009)

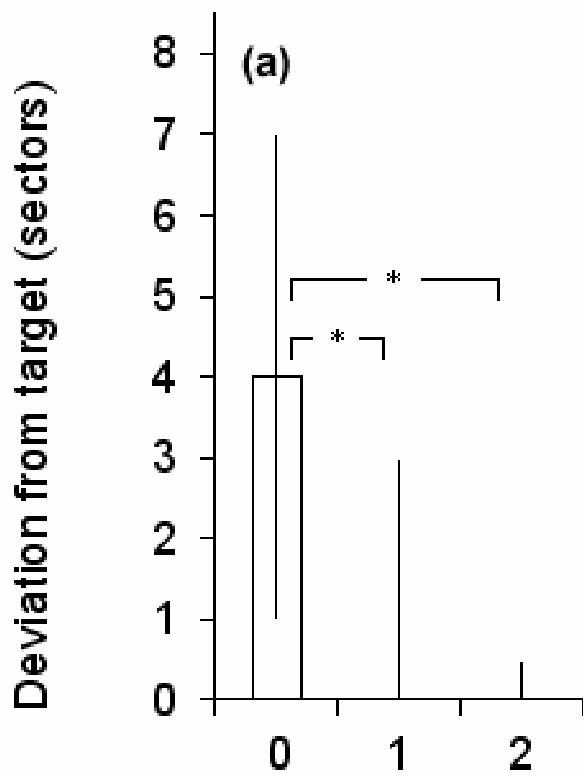
Groups of 8 individuals have to evacuate an area but remain together



Humans

Leadership

a small minority can lead without active signaling

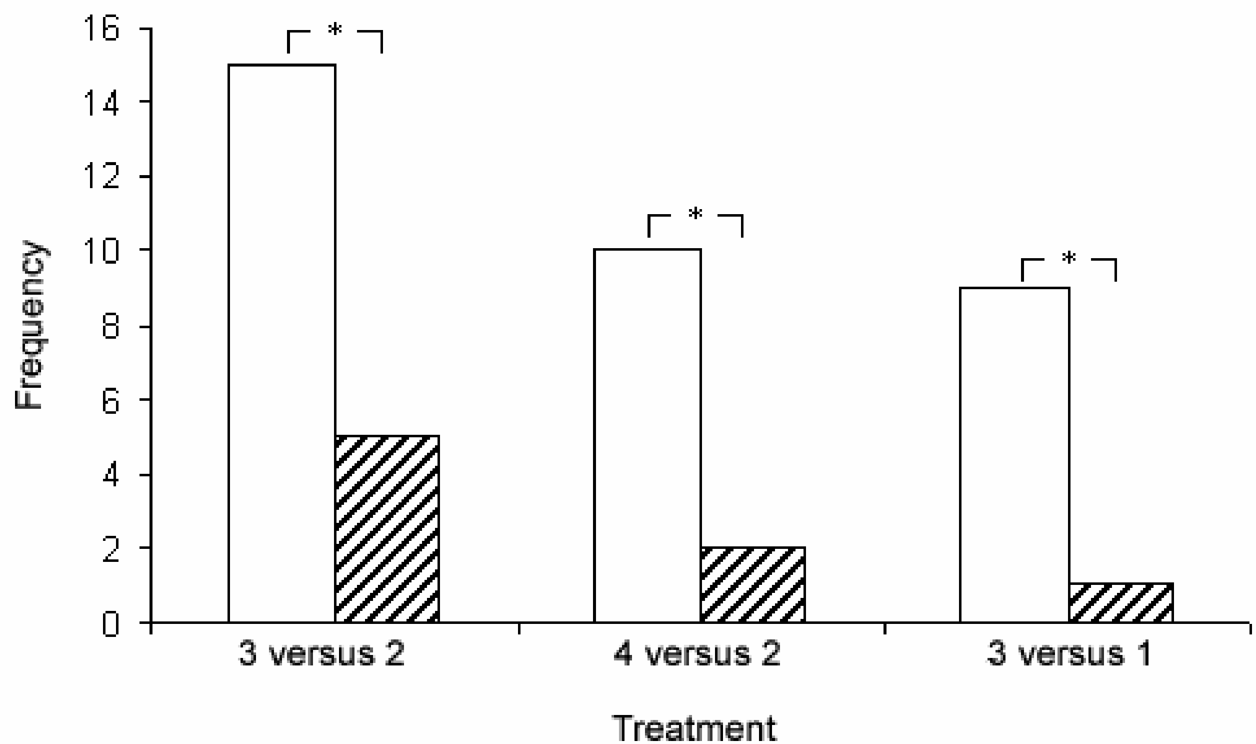


Collective decision-making

Humans

Collective decision-making

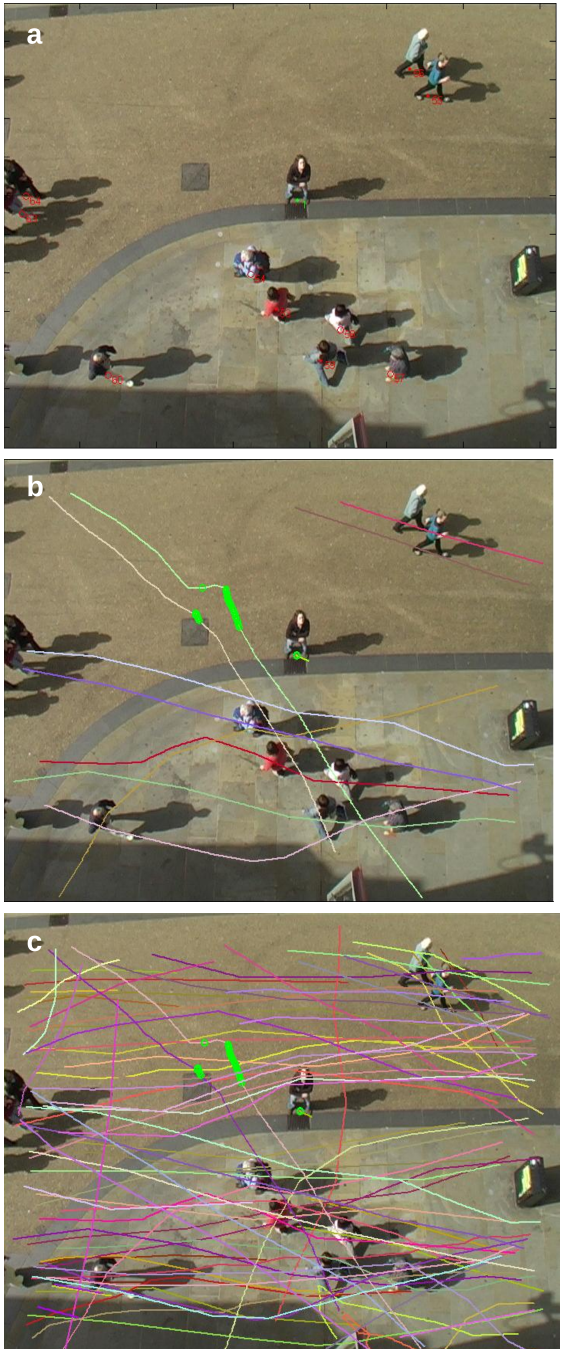
When conflicting directional information is given the majority dictate the direction of the group



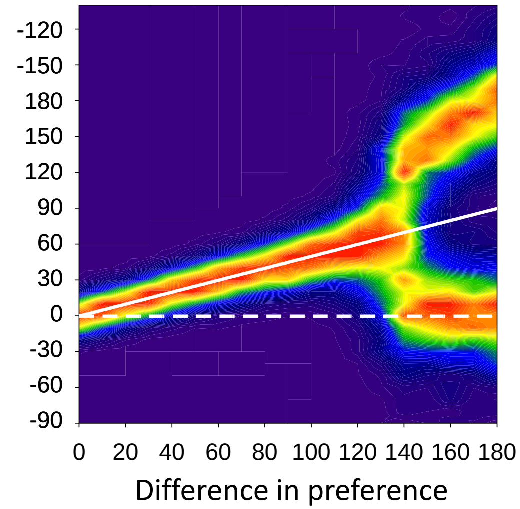
Humans

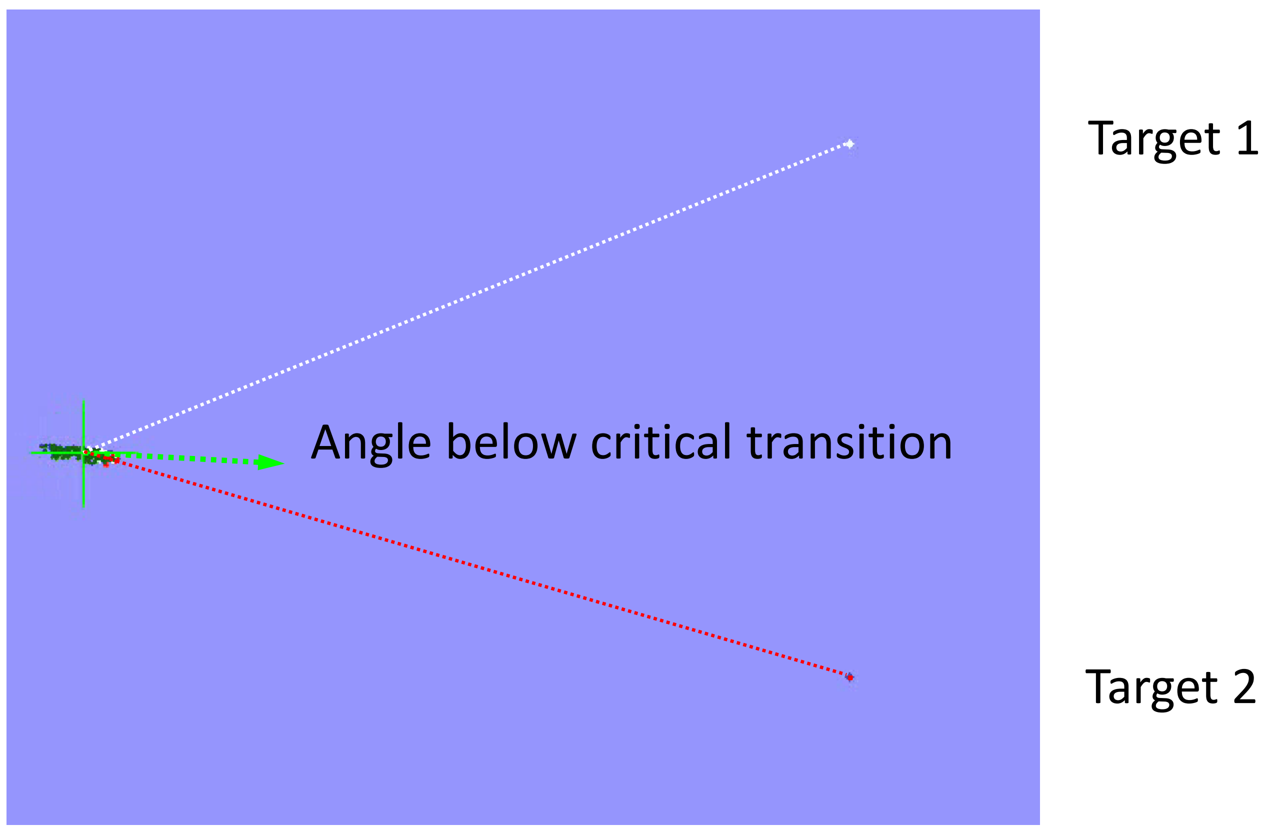
Large groups

Collective decision-making

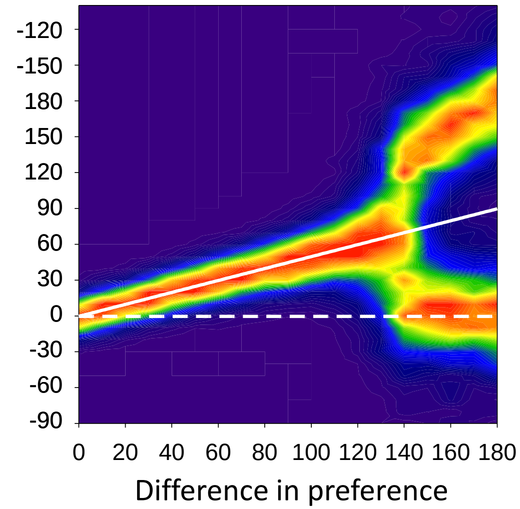


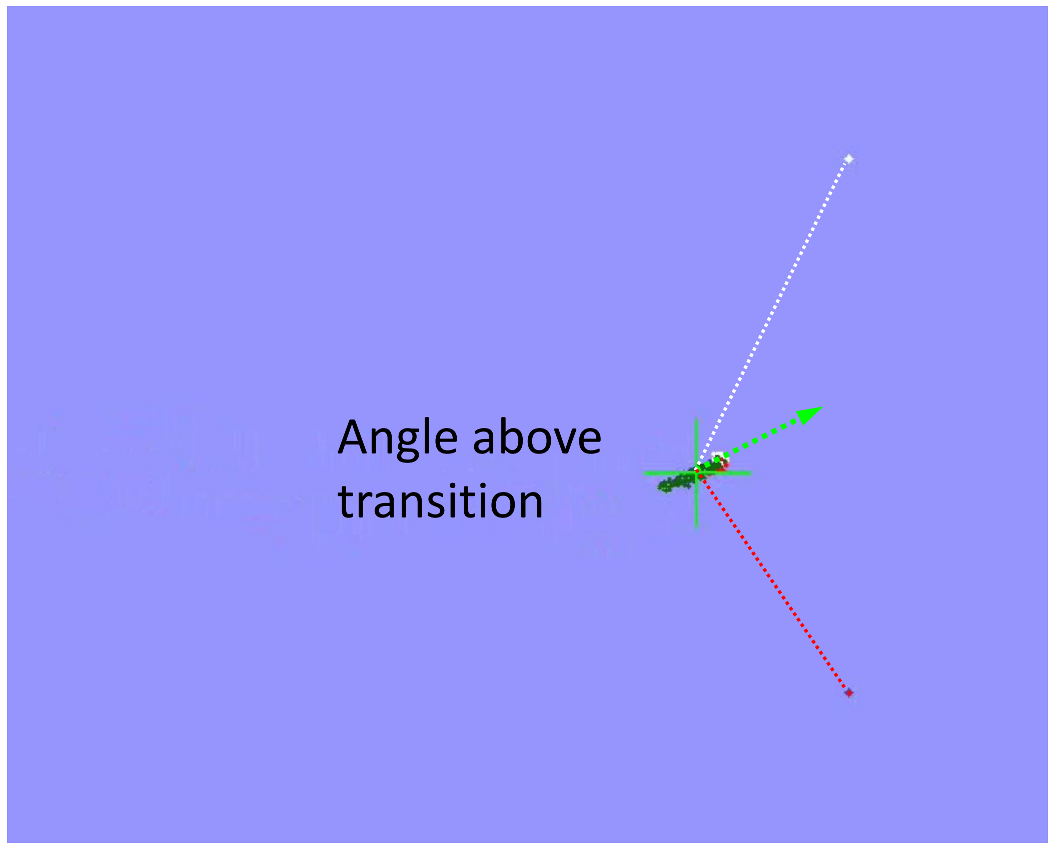
Collective decision-making





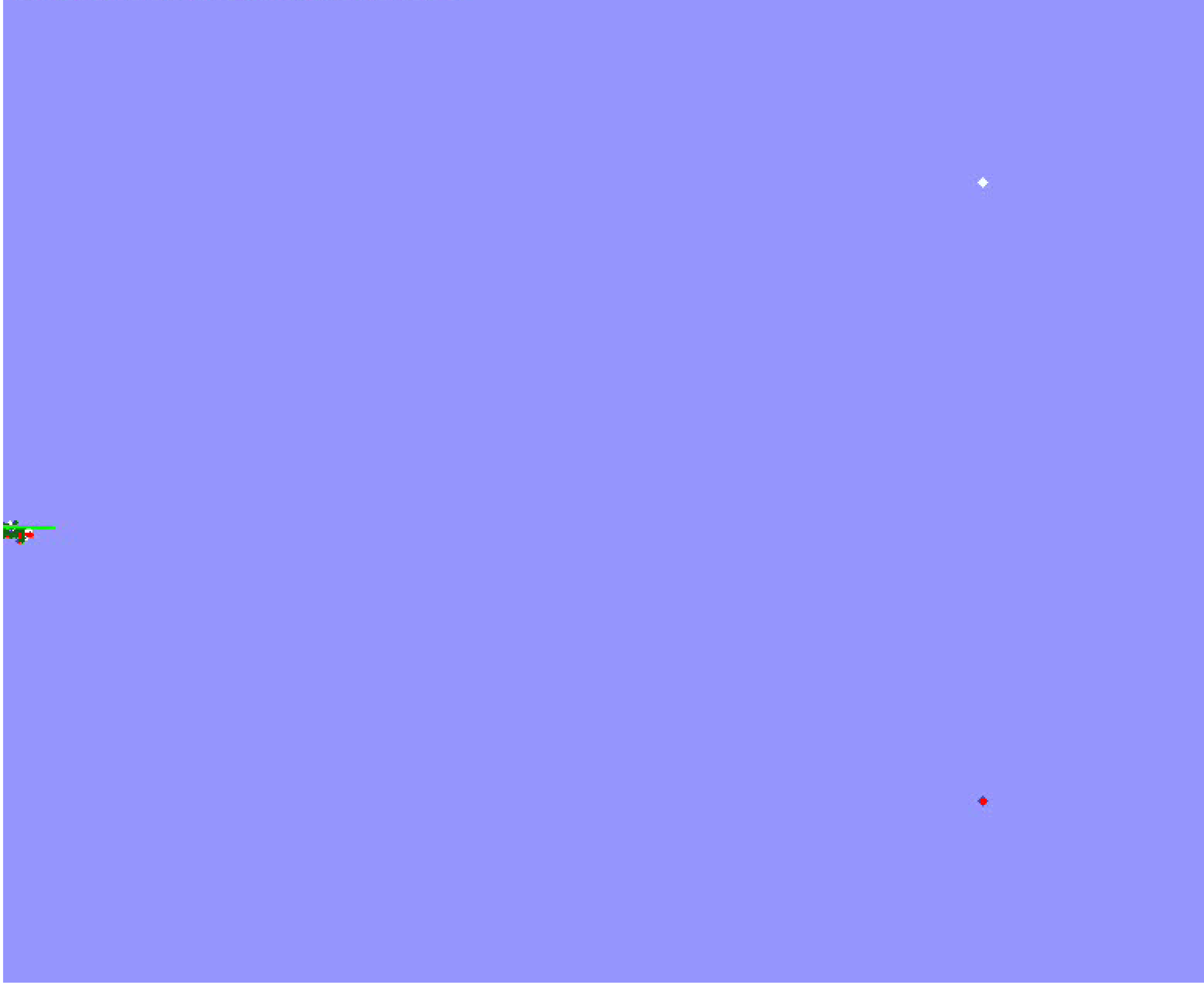
Collective decision-making

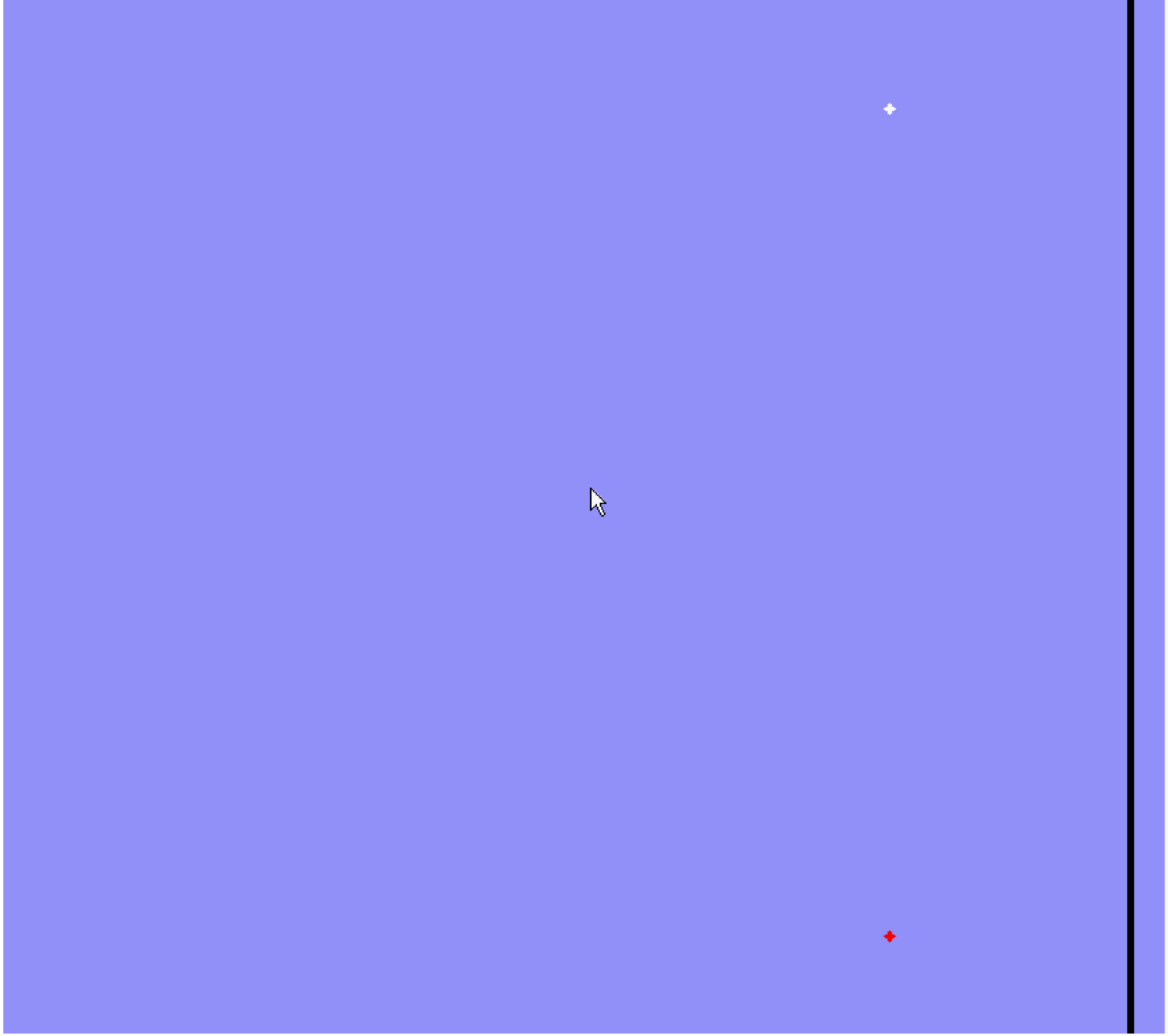


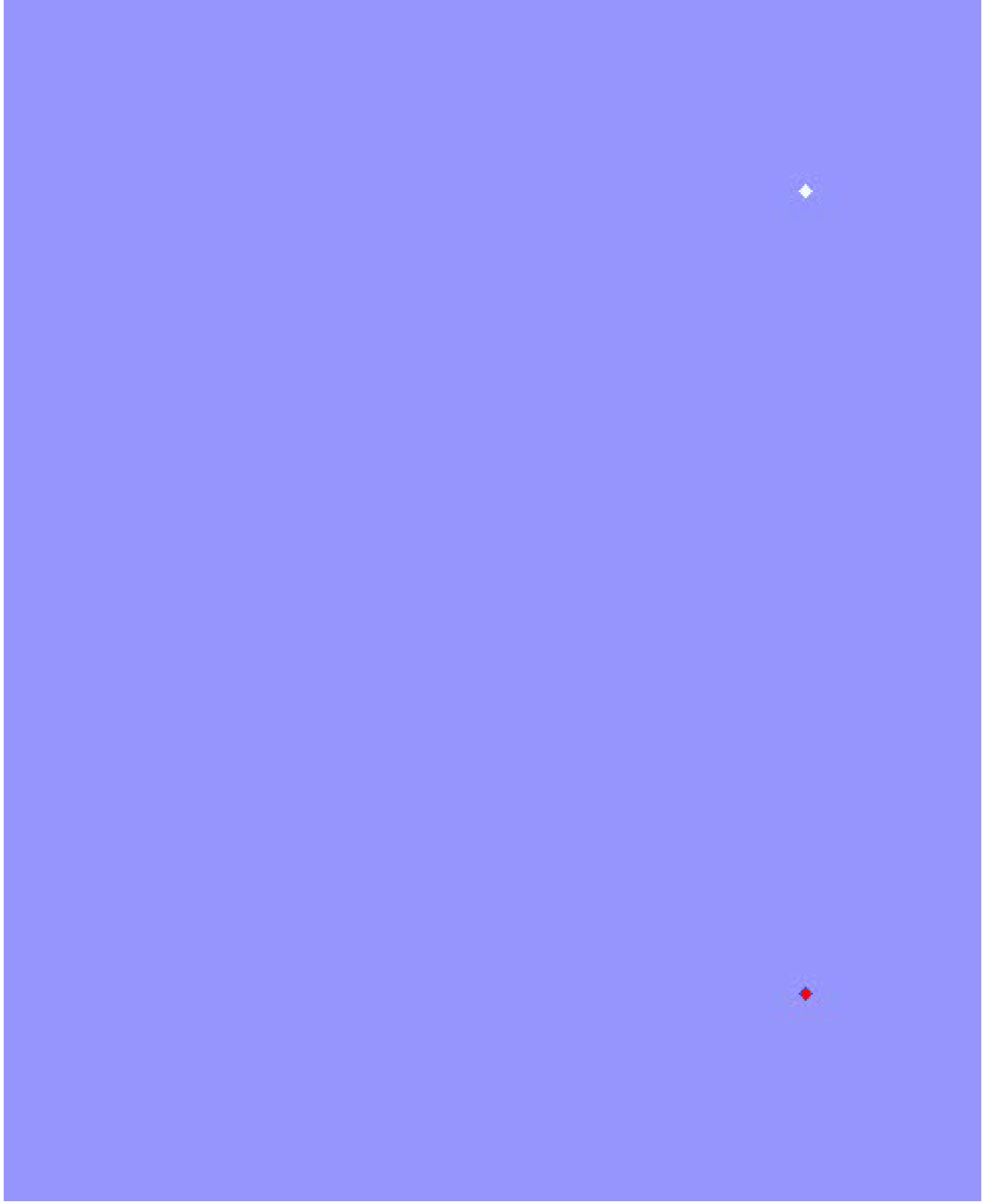


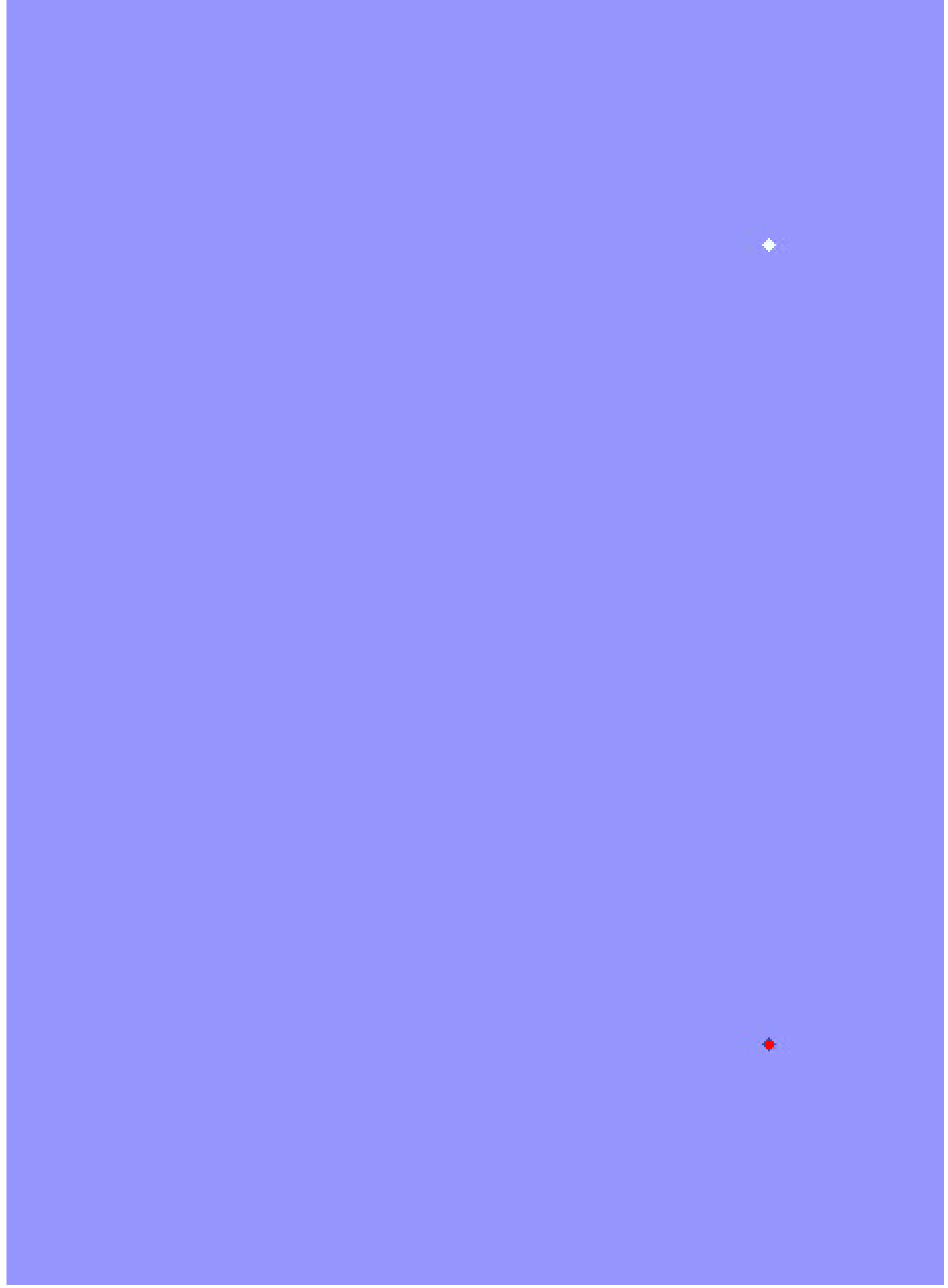
Target 1

Target 2









Collective decision-making

J Nonlinear Sci
DOI 10.1007/s00332-008-9038-6

Journal of Nonlinear Science

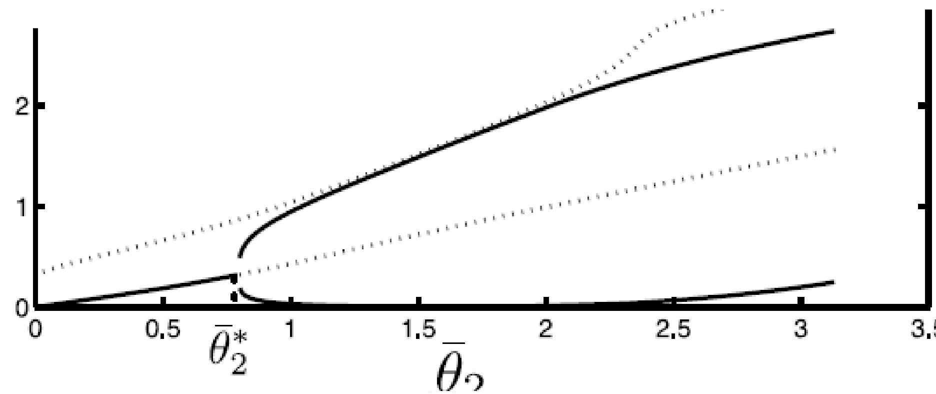
Dynamics of Decision Making in Animal Group Motion

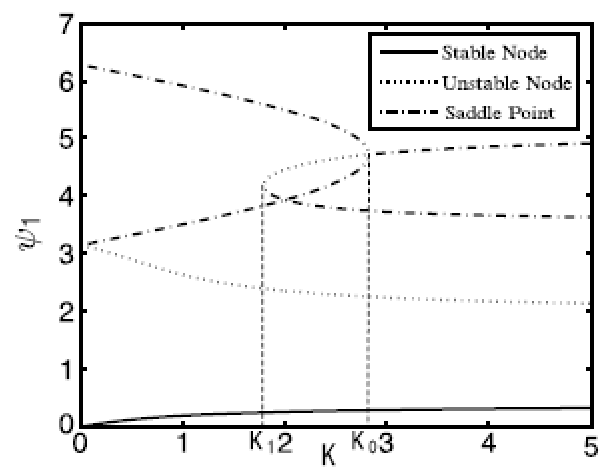
Benjamin Nabet · Naomi E. Leonard ·
Iain D. Couzin · Simon A. Levin

$$\dot{\theta}_j = \sin(\bar{\theta}_1 - \theta_j) + \frac{K}{N}\sum_{l=1}^{N}\sin(\theta_l - \theta_j), \quad j \in \mathcal{N}_1,$$

$$\dot{\theta}_j = \sin(\bar{\theta}_2 - \theta_j) + \frac{K}{N}\sum_{l=1}^{N}\sin(\theta_l - \theta_j), \quad j \in \mathcal{N}_2,$$

$$\dot{\theta}_j = \frac{K}{N}\sum_{l=1}^{N}\sin(\theta_l - \theta_j), \quad j \in \mathcal{N}_3\,.$$





Very little is known about what mechanisms are used for collective decision-making in vertebrate groups

Collective decision-making

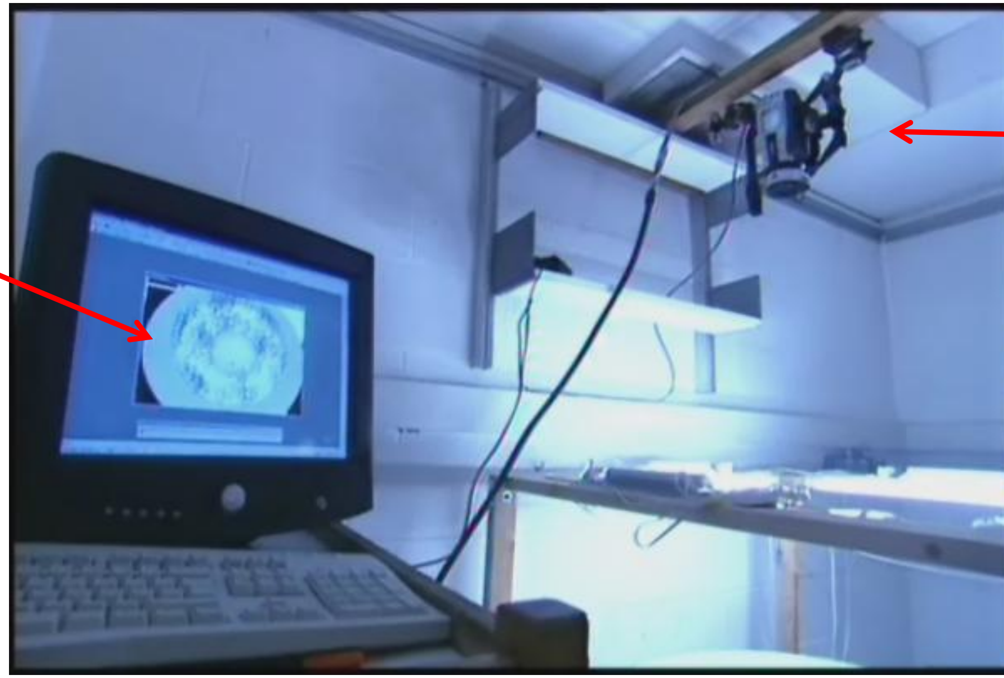
With Ashley Ward, David Sumpter & Jens Krause

Collective decision-making

Collective decision-making

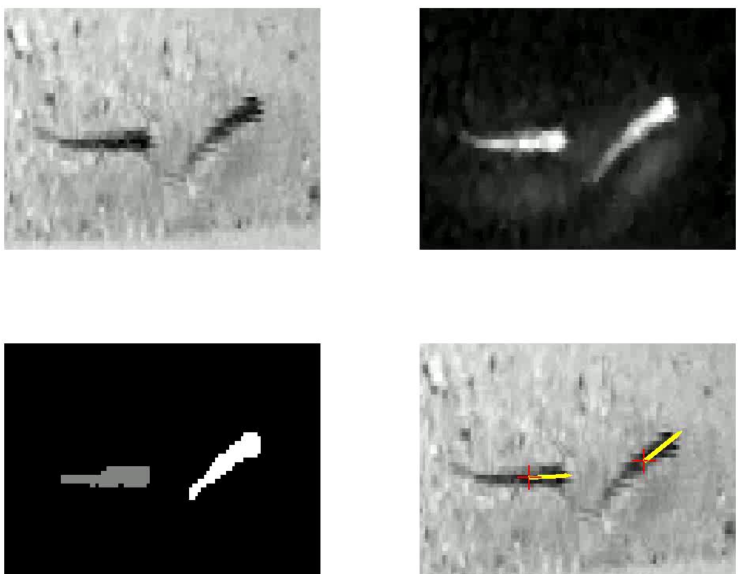
With Ashley Ward, David Sumpter & Jens Krause

Tracking Software – *extract data in real-time*



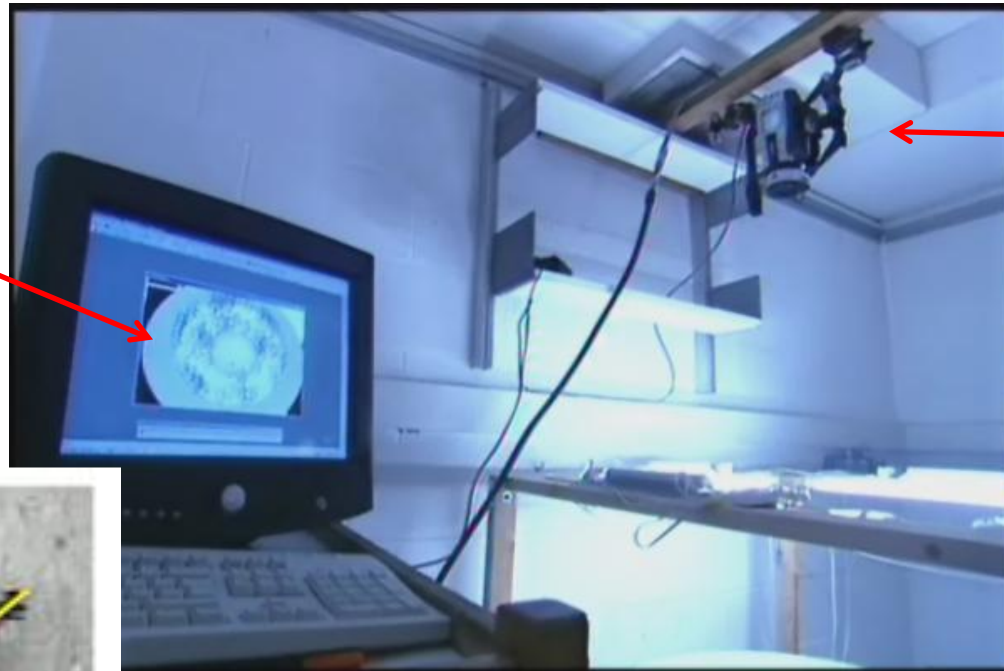
Tracking camera

Experimental arena



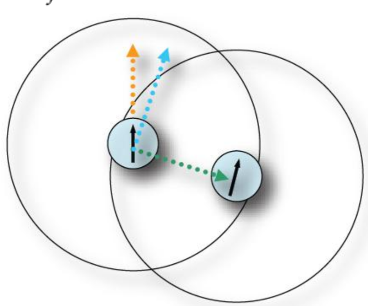
Collective decision-making

Tracking
Software –
extract data
in real-time



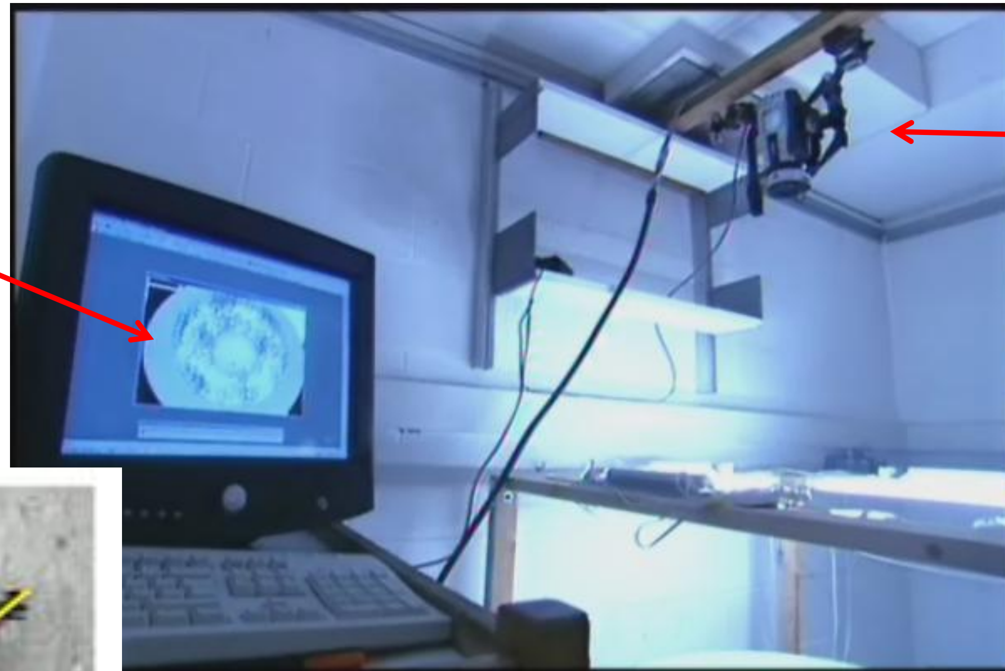
Tracking
camera

$$\mathbf{d}_i(t+\Delta t) = \sum_{j\neq i} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{|(\mathbf{c}_j(t) - \mathbf{c}_i(t))|} + \sum_{j=1} \frac{\mathbf{v}_j(t)}{|\mathbf{v}_j(t)|}$$



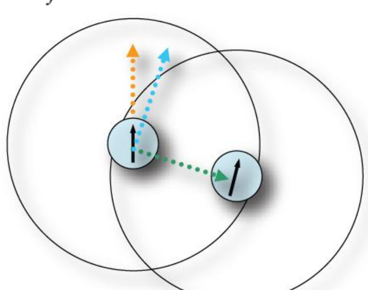
Collective decision-making

Tracking Software – *extract data in real-time*



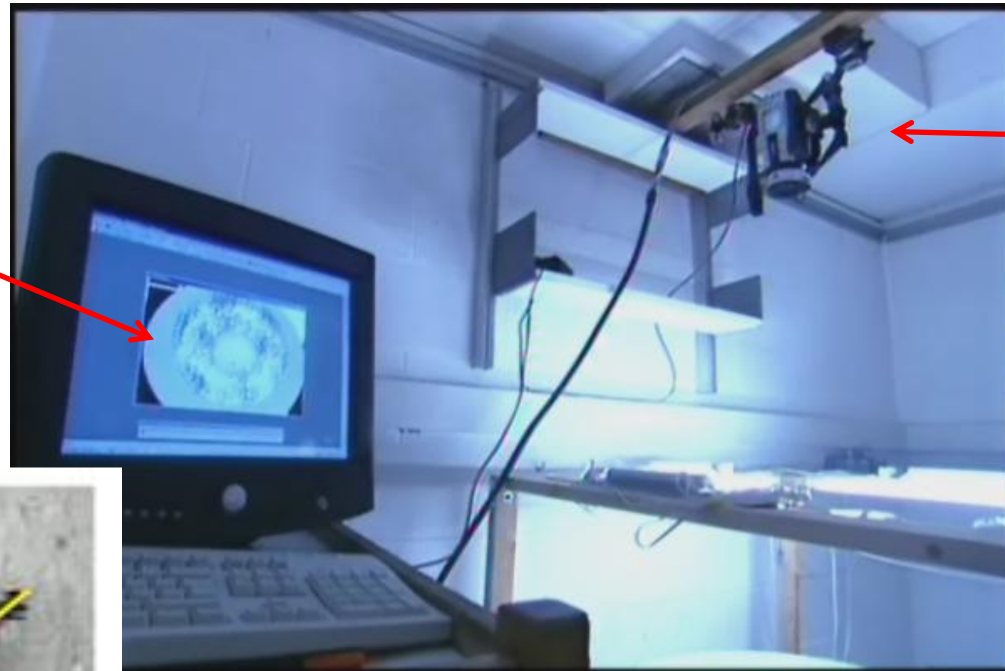
Tracking camera

$$\mathbf{d}_i(t+\Delta t) = \sum_{j\neq i} \frac{\mathbf{c}_j(t)-\mathbf{c}_i(t)}{|(\mathbf{c}_j(t)-\mathbf{c}_i(t))|} + \sum_{j=1} \frac{\mathbf{v}_j(t)}{|\mathbf{v}_j(t)|}$$



Collective decision-making

Tracking
Software –
extract data
in real-time



Tracking
camera

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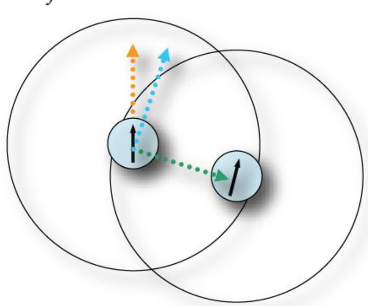
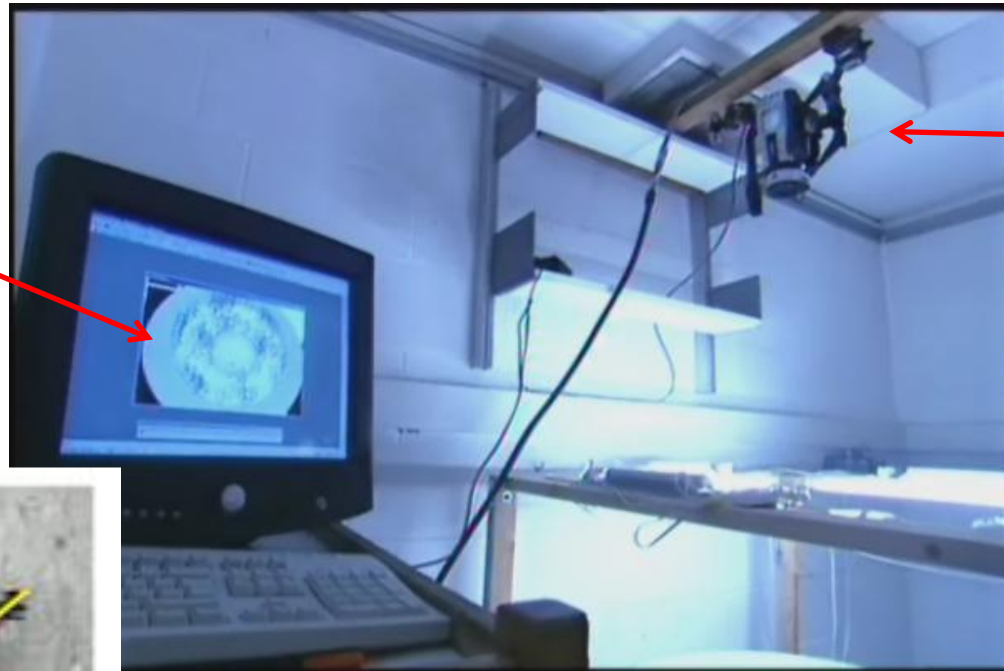


Collective decision-making

Tracking Software – *extract data in real-time*



Tracking camera

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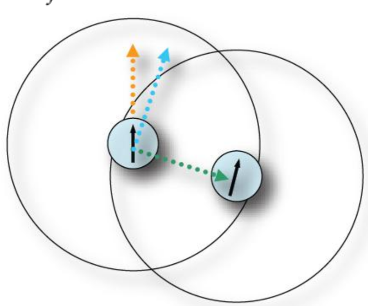
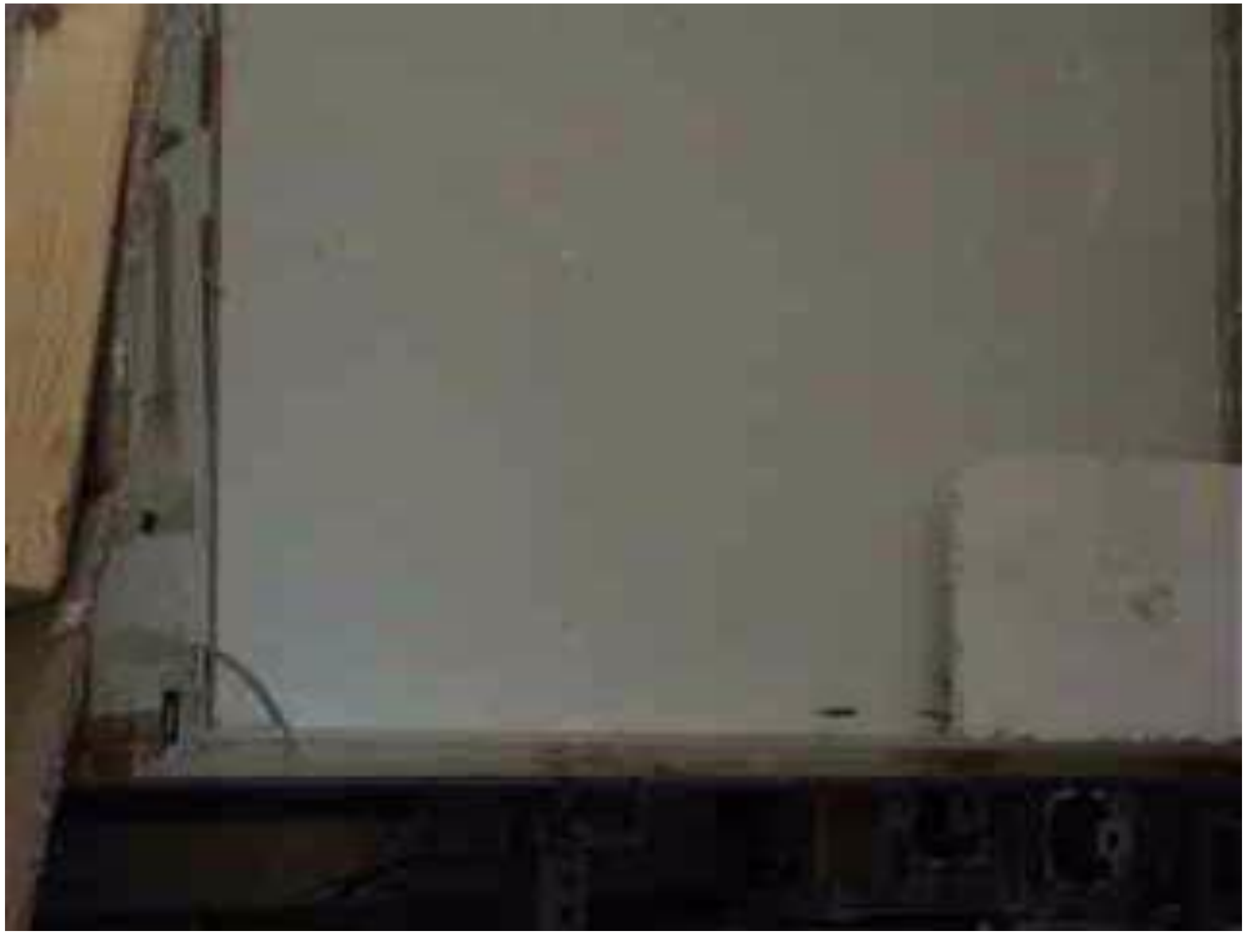


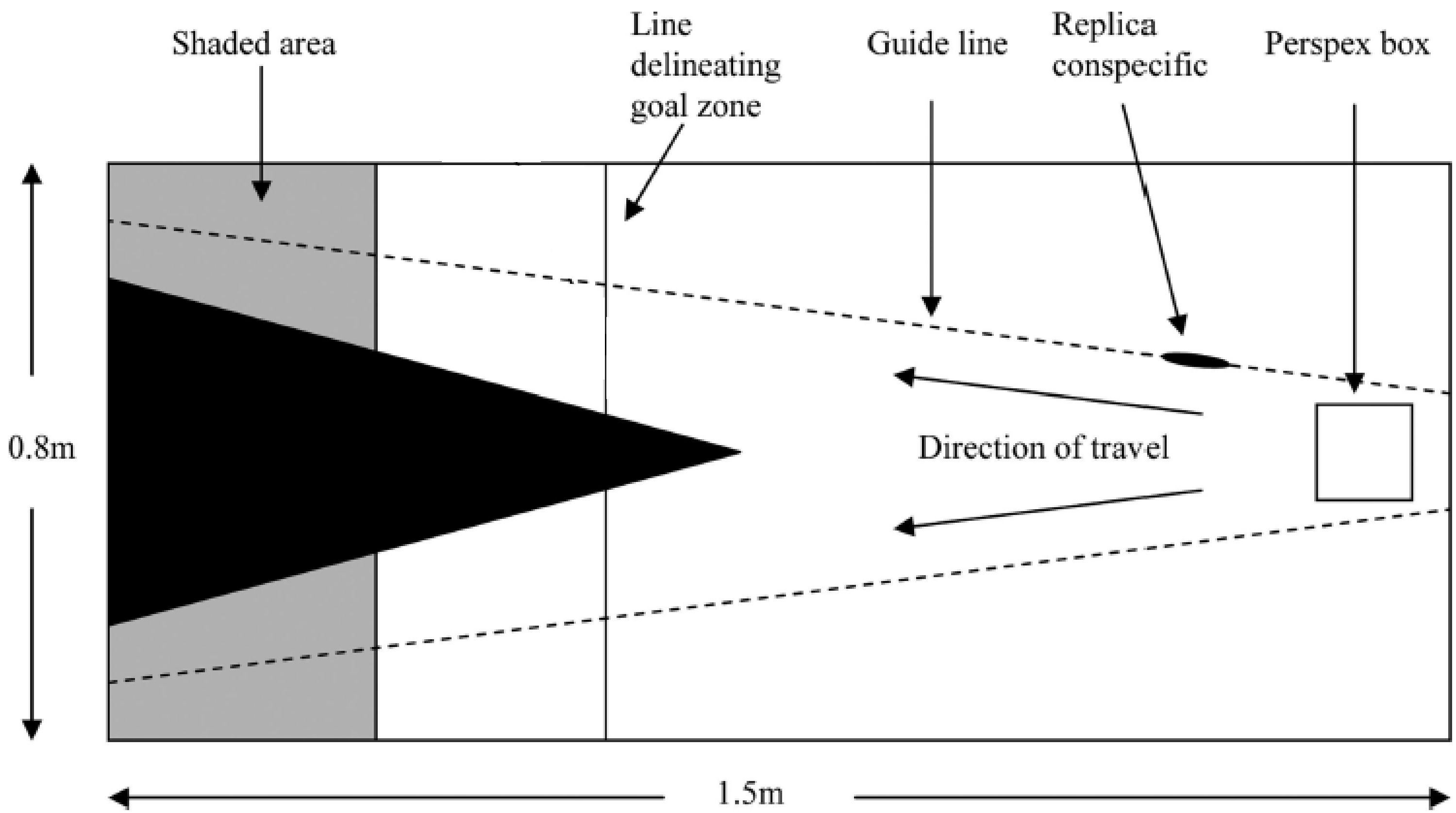
16 x

Jens Krause, Jolyon Faria & John Dyer



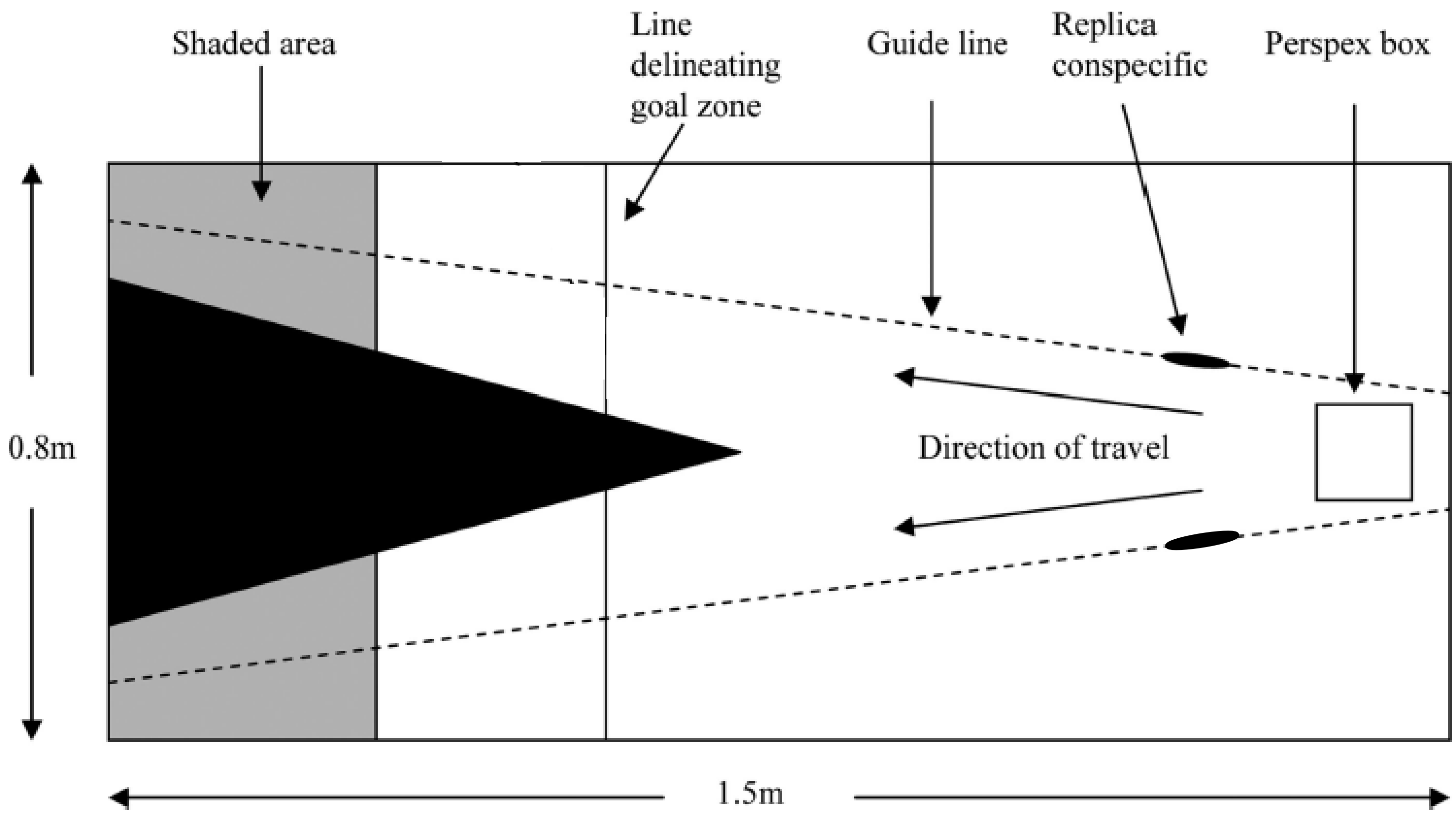
Collective decision-making

Ashley Ward, David Sumpter *Proc. Natl. Acad. Sci. USA* (2008) **105**, 6948-6953

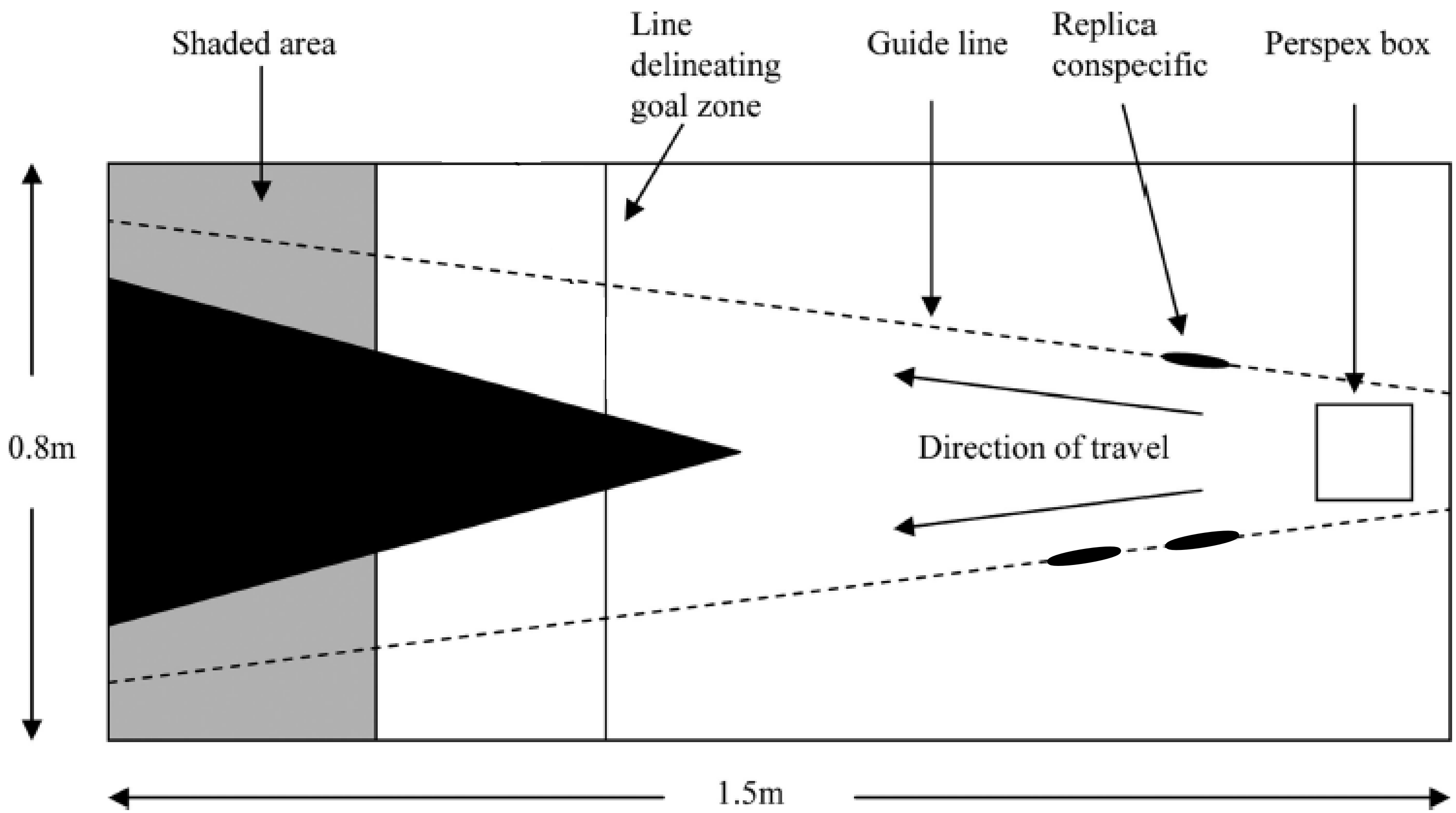


Ashley Ward, David Sumpter

Proc. Natl. Acad. Sci. USA (2008) **105**, 6948-6953

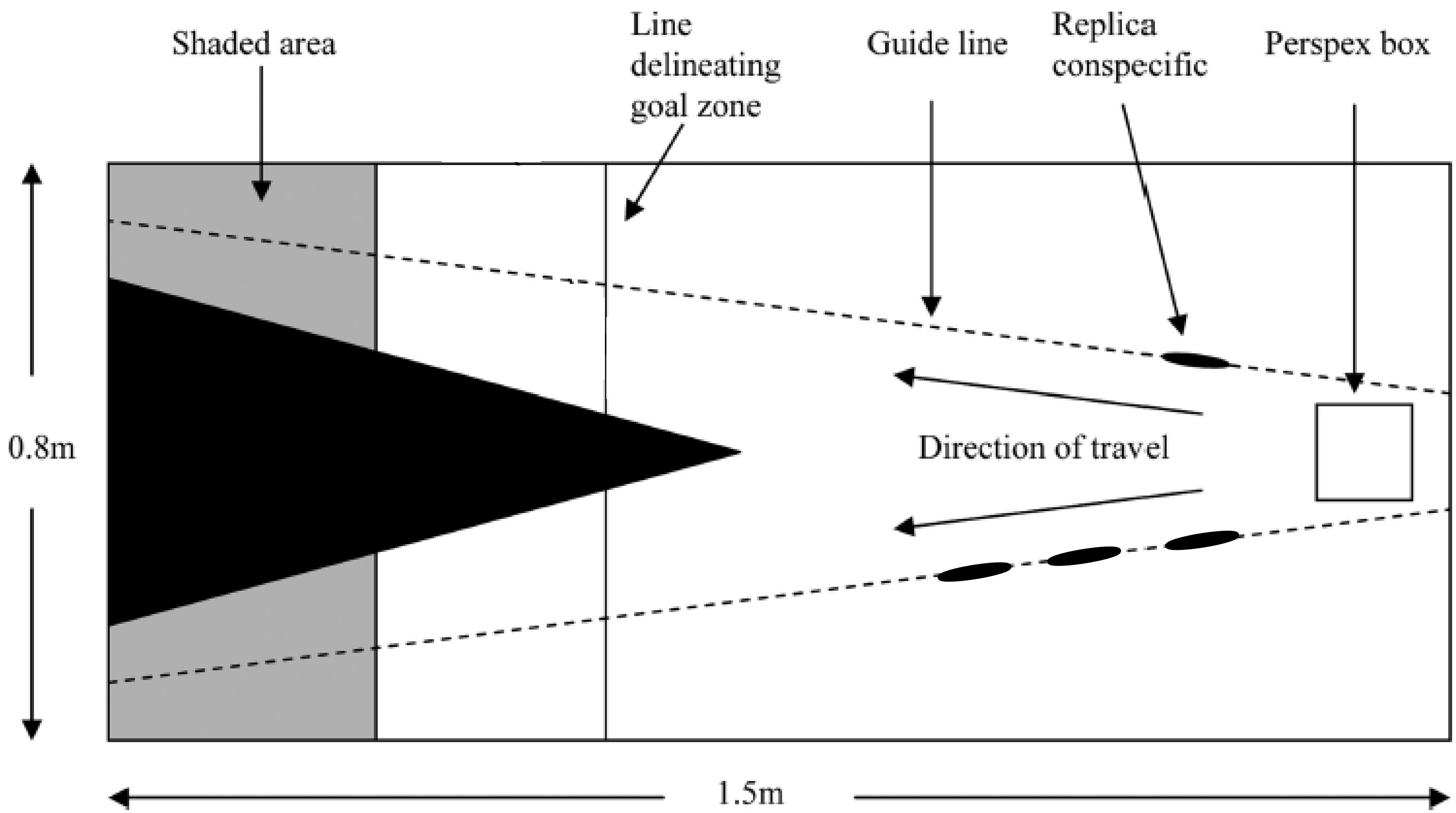


Ashley Ward, David Sumpter *Proc. Natl. Acad. Sci. USA* (2008) **105**, 6948-6953



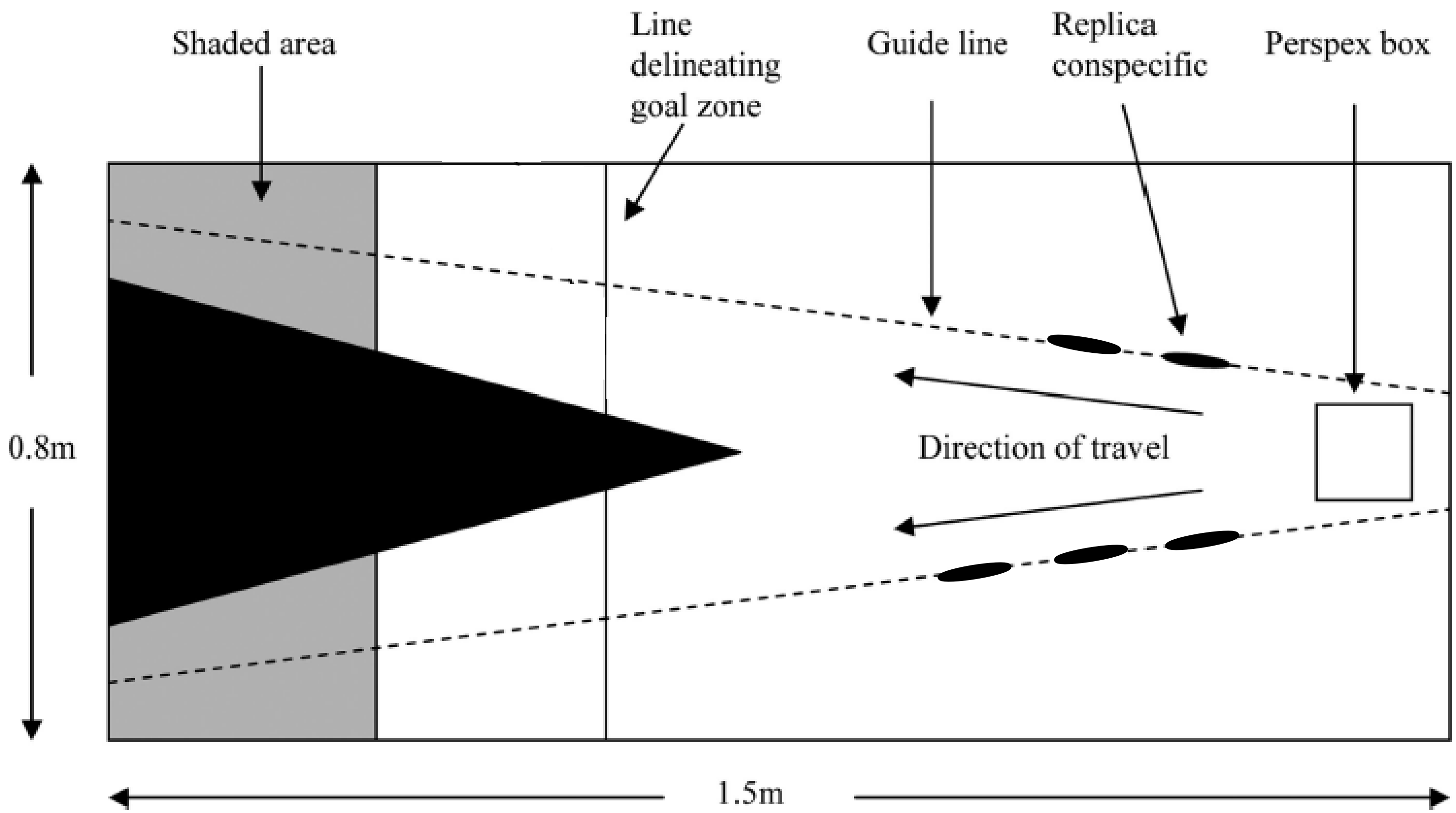
Ashley Ward, David Sumpter

Proc. Natl. Acad. Sci. USA (2008) **105**, 6948-6953



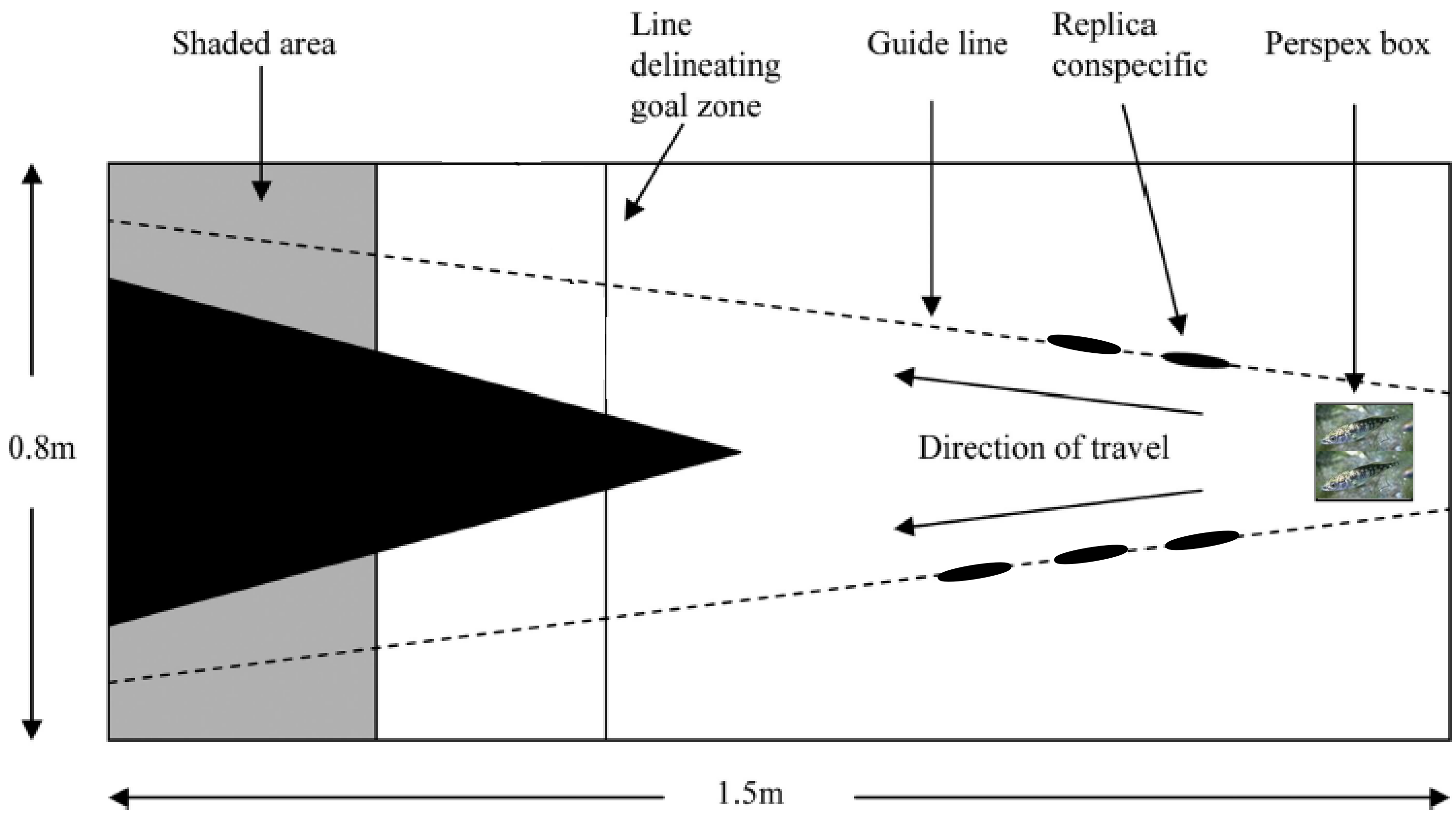
Ashley Ward, David Sumpter

Proc. Natl. Acad. Sci. USA (2008) **105**, 6948-6953

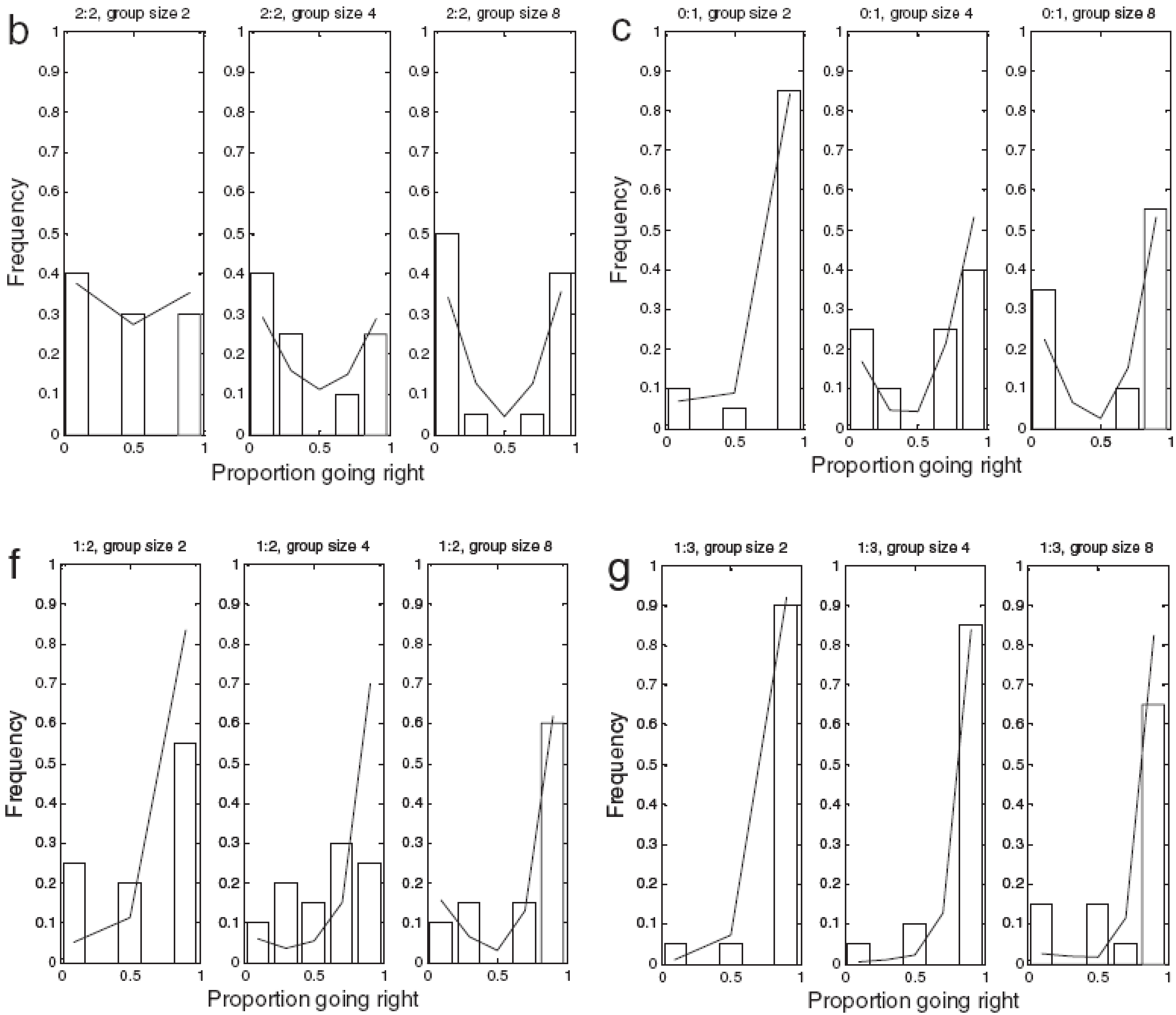


Collective decision-making

Ashley Ward, David Sumpter *Proc. Natl. Acad. Sci. USA* (2008) **105**, 6948-6953



Collective decision-making



Simple model

In the absence of other individuals taking a particular direction, uncommitted individuals have a spontaneous probability of choosing either direction based on their own information – parameterized by individual experiments (***independent***)

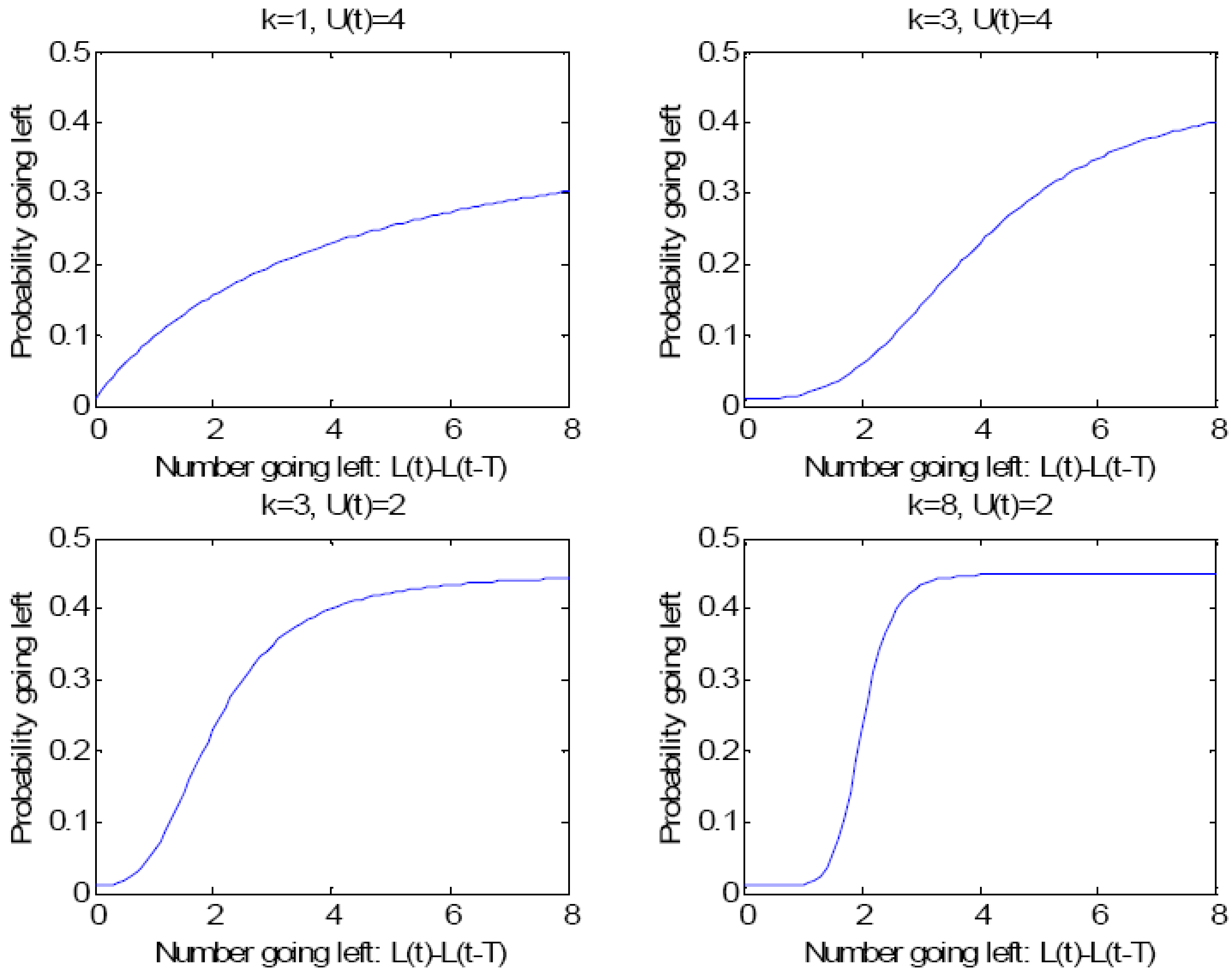
However their probability of choosing one direction increases as a function of the number of individuals that have recently gone that way (***social***)

Two main parameters determine the shape of this response:

a – spontaneous accept rate

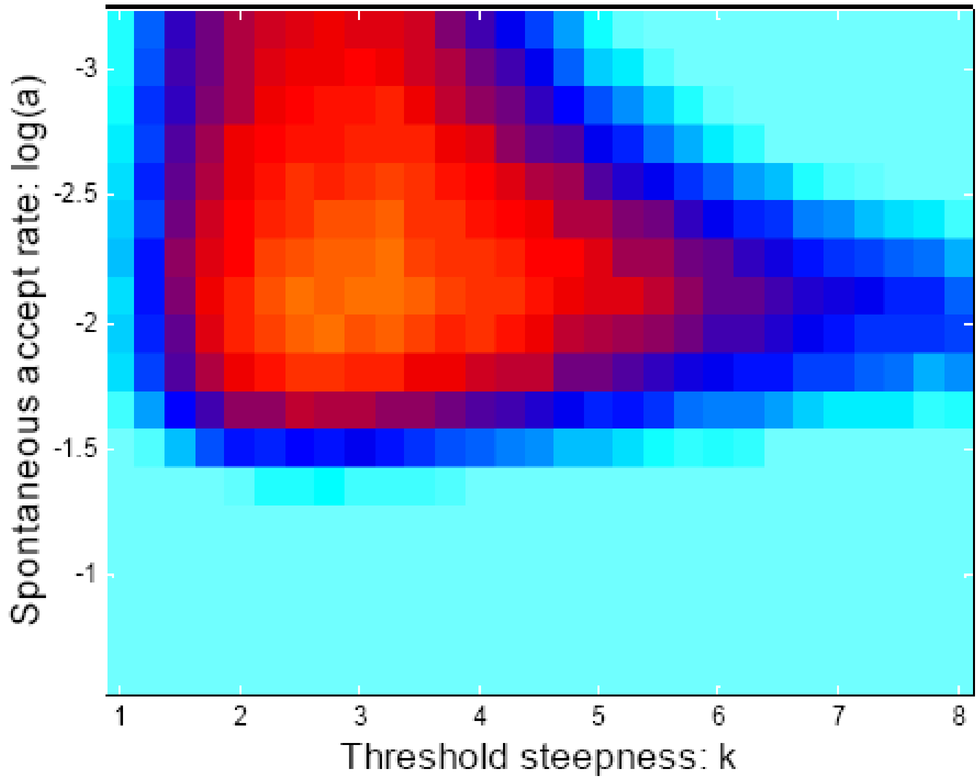
k – the steepness of the response

Collective decision-making



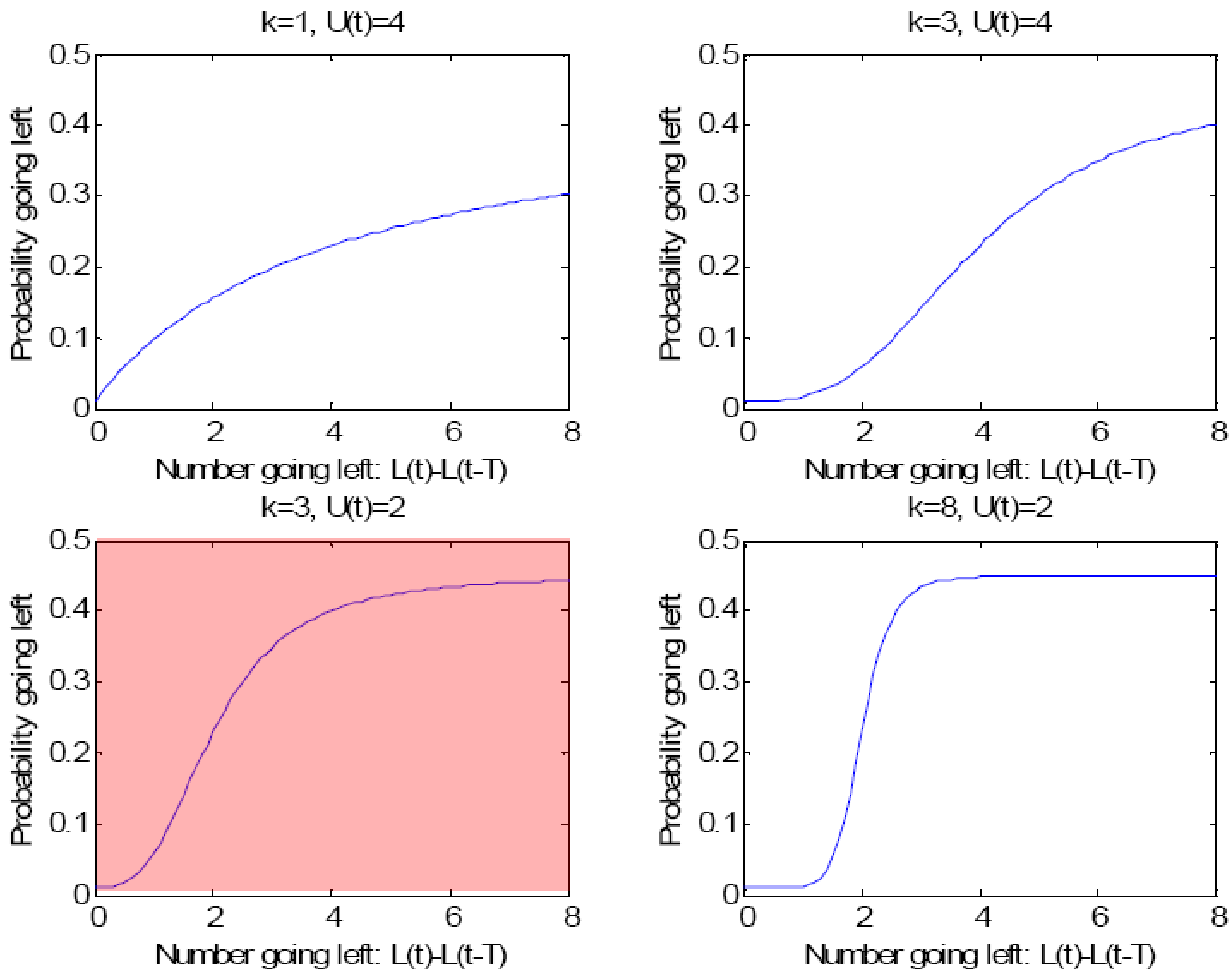
Collective decision-making

Model fit to data

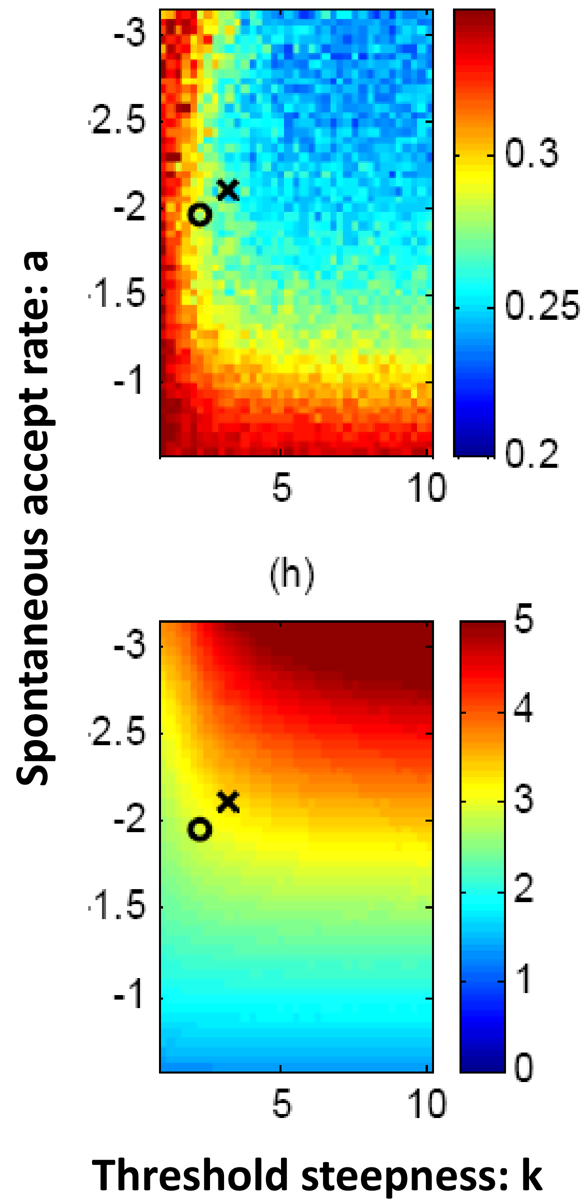


Quorum decision-making in fish schools

Collective decision-making



x = data



Error rate

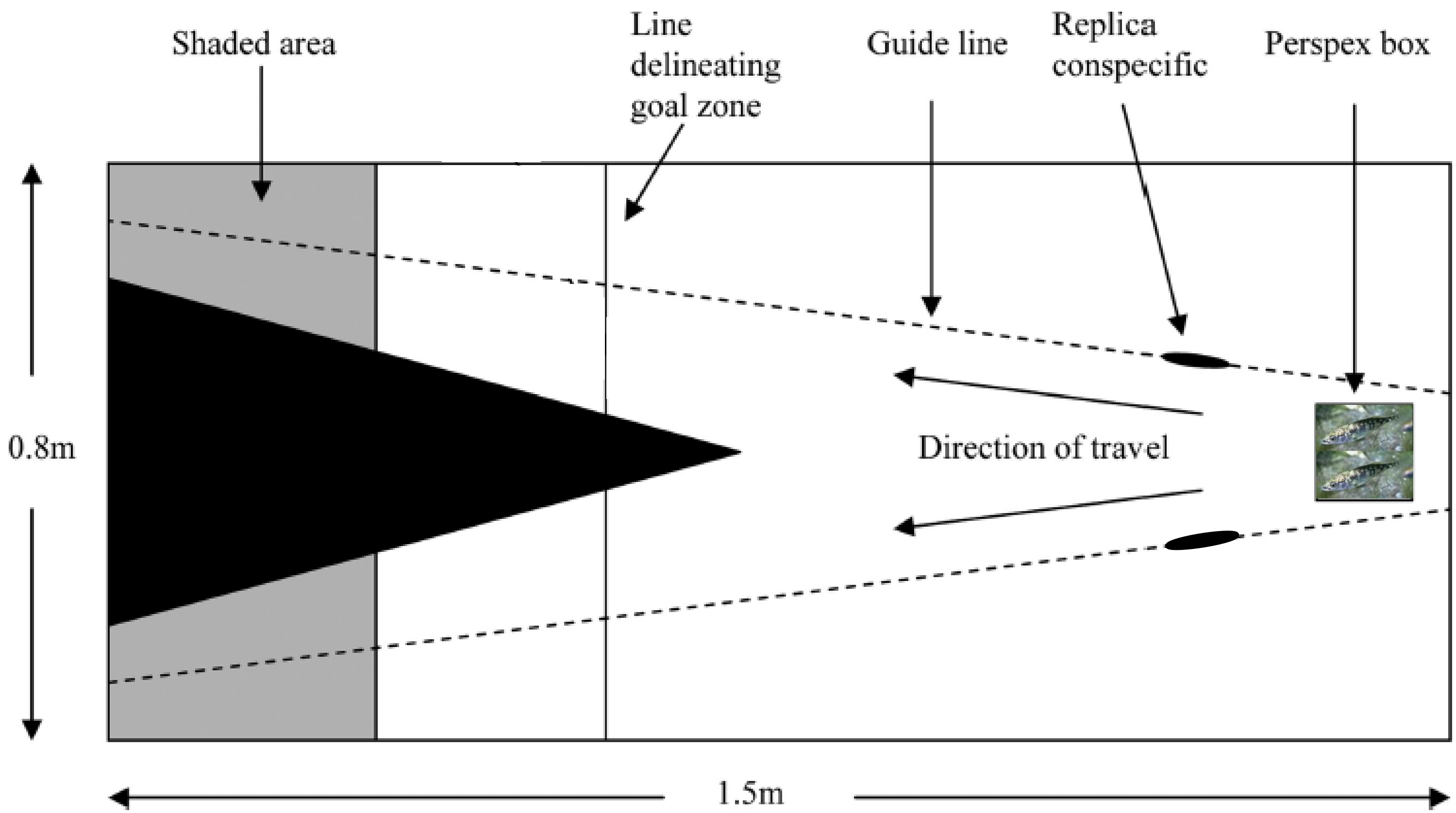
Time taken

Collective decision-making

With David Sumpter, Ashley Ward & Jens Krause

Current Biology (2008) **18(22)**, 1773-1777

Collective decision-making

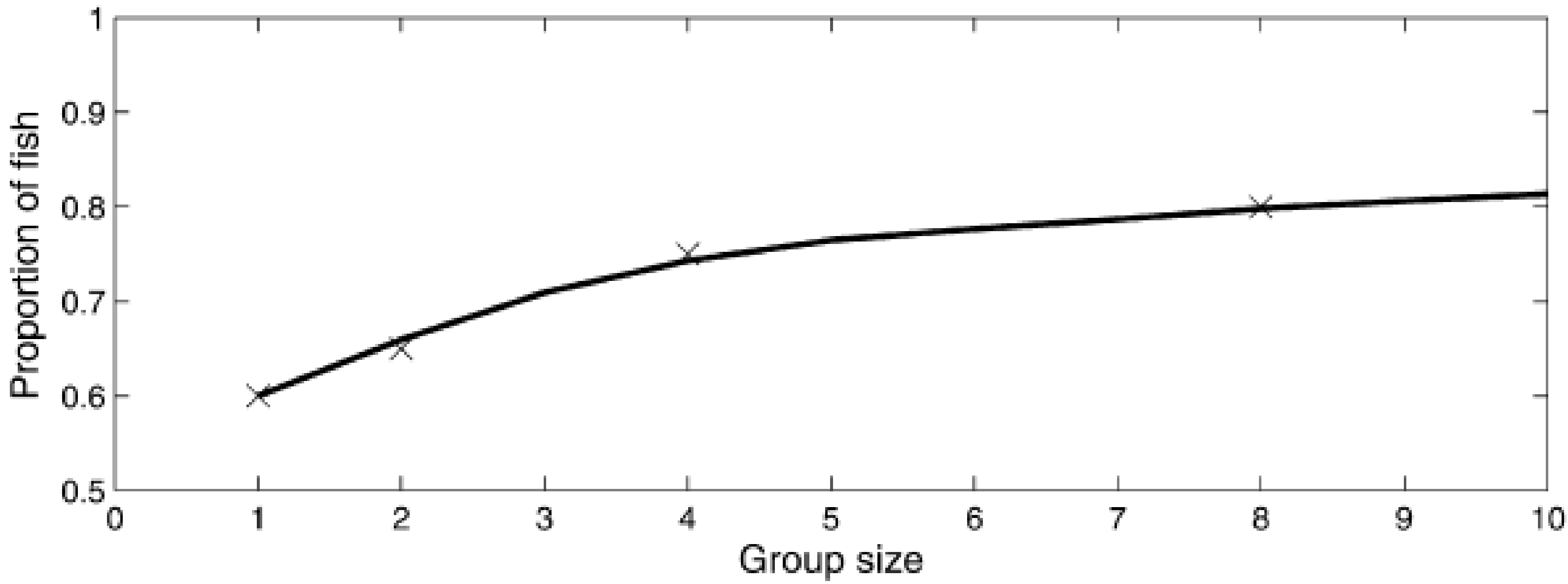


Collective decision-making

With David Sumpter, Ashley Ward & Jens Krause

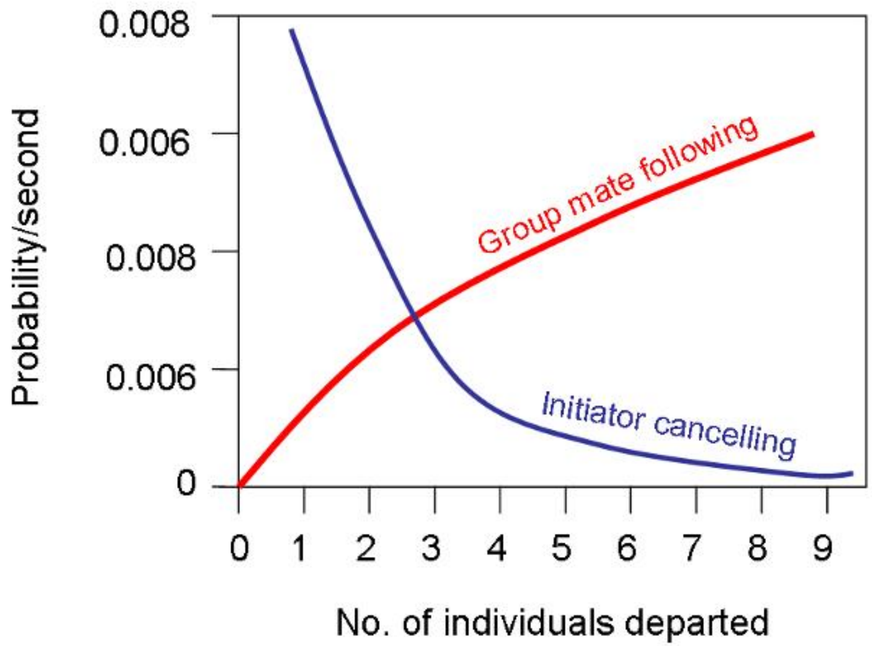
Current Biology (2008) **18(22)**, 1773-1777

Proportion of fish making a ‘correct’ choice



Collective decision-making

Petit, O., Gautrais, J., Leca, J-B., Theraulaz, G., & Deneubourg, J. L. (in press) Collective decision-making in white-faced capuchins. Proceedings of the Royal Society, Series B.



Marie-Helene Pilot, Jean-Louis Deneubourg

Humans

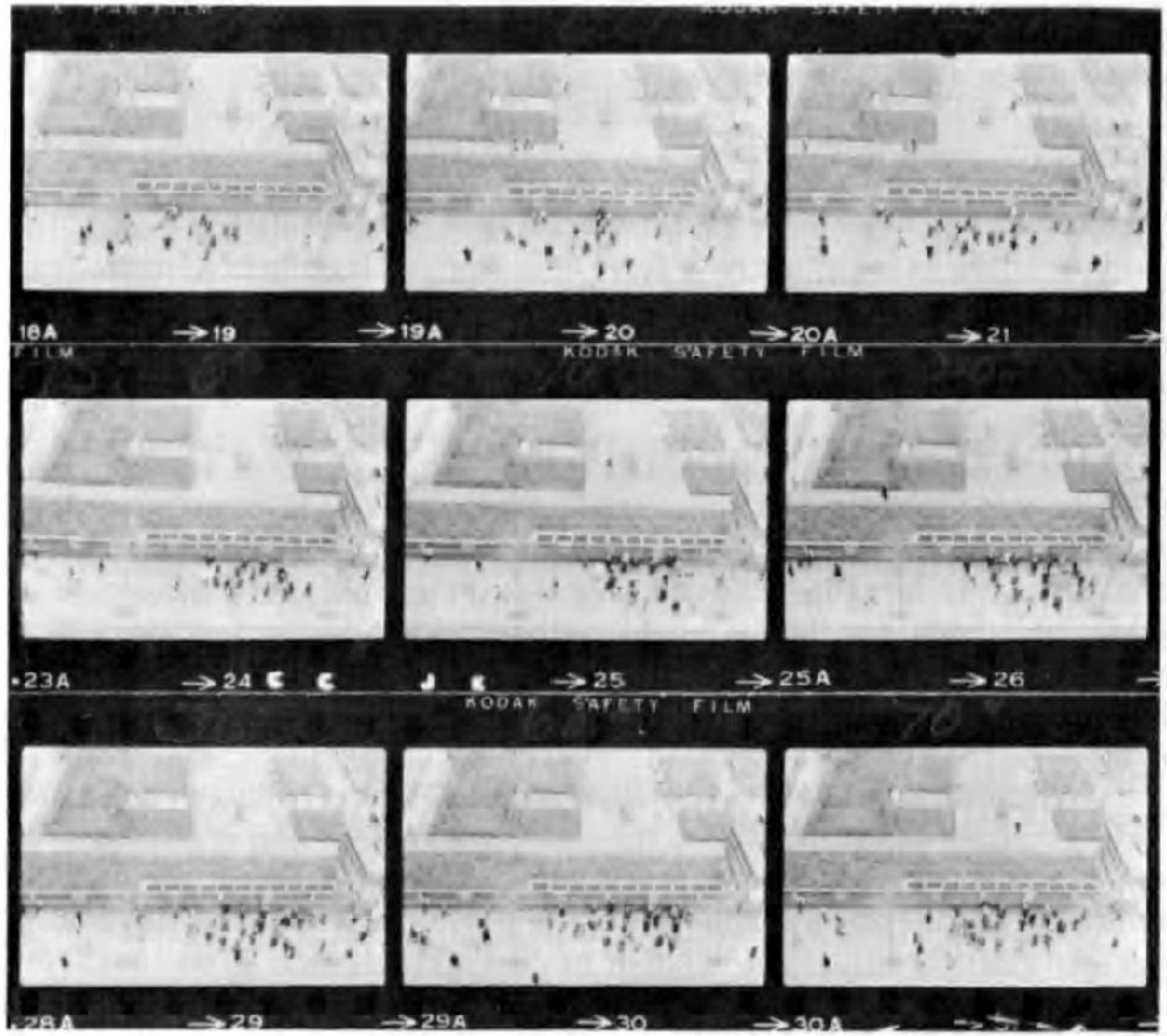
Threshold Models of Collective Behavior[1]

Mark Granovetter
State University of New York at Stony Brook

The American Journal of Sociology, Vol. 83, No. 6 (May, 1978), pp. 1420-1443

Humans

Stanley Milgram, Leonard Bickman and Lawrence Berkowitz **(1969)** Note on the drawing power of crowds of different size.
Journal of Personality and Social Psychology, **13**(2), 79-82



Collective decision-making

Humans

Stanley Milgram, Leonard Bickman and Lawrence Berkowitz **(1969)** Note on the drawing power of crowds of different size.
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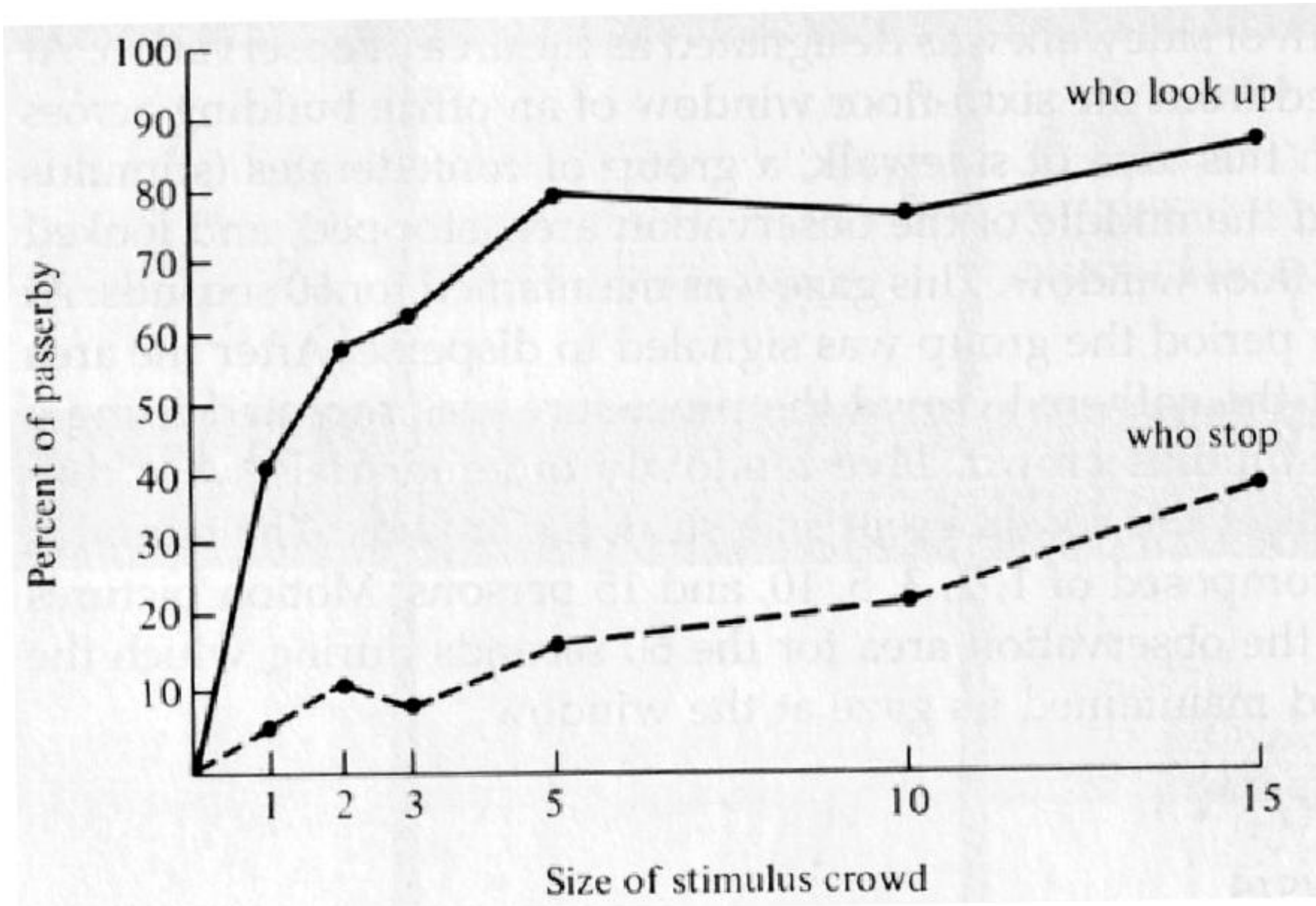
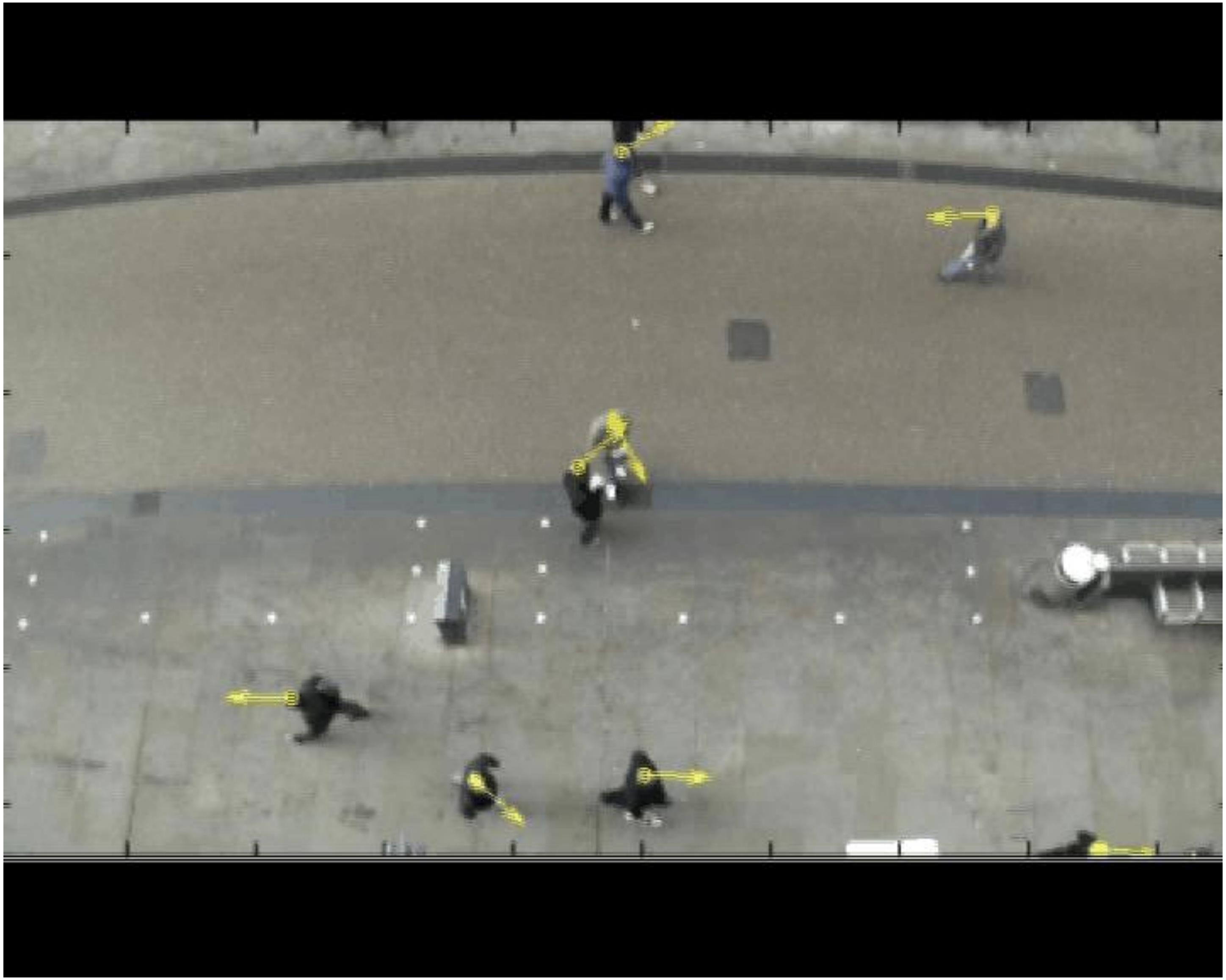


Collective decision-making



with Joe Hale and Simon Garnier

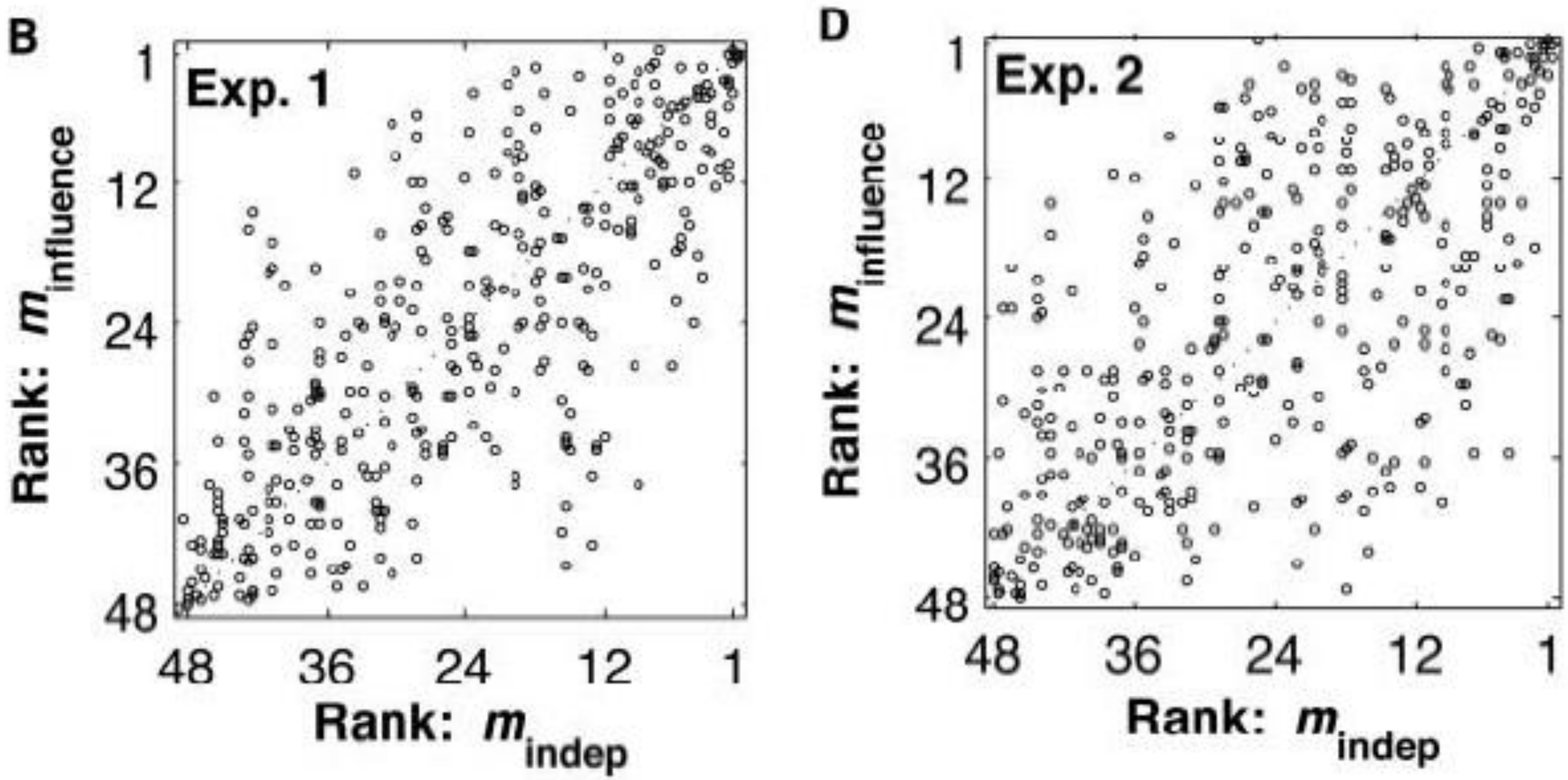
Collective decision-making

Collective decision-making

REPORTS 10 FEBRUARY 2006 VOL 311 SCIENCE

Experimental Study of Inequality and Unpredictability in an Artificial Cultural Market

Matthew J. Salganik,[1,2*] Peter Sheridan Dodds,[2*] Duncan J. Watts[1,2,3*]



Collective decision-making

CITY EDITION

London Herald

LATE PRICES

FRIDAY 25th OCTOBER 1929

WALL STREET CRASH!

Black Thursday in America

Stocks Plunge and Eleven Commit Suicide

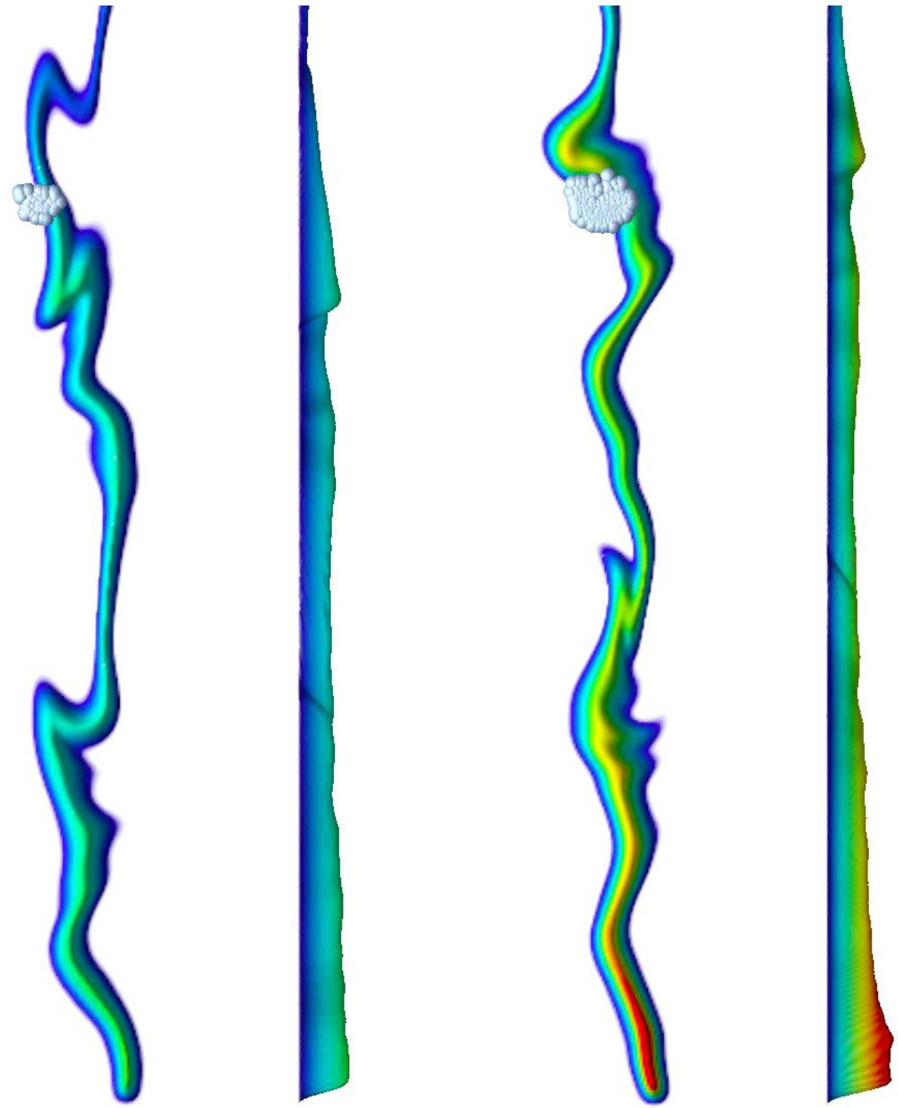
What Went Wrong?

OTHER NEWS

COLEMAN'S

Evolution of collective behavior

Evolution of migration

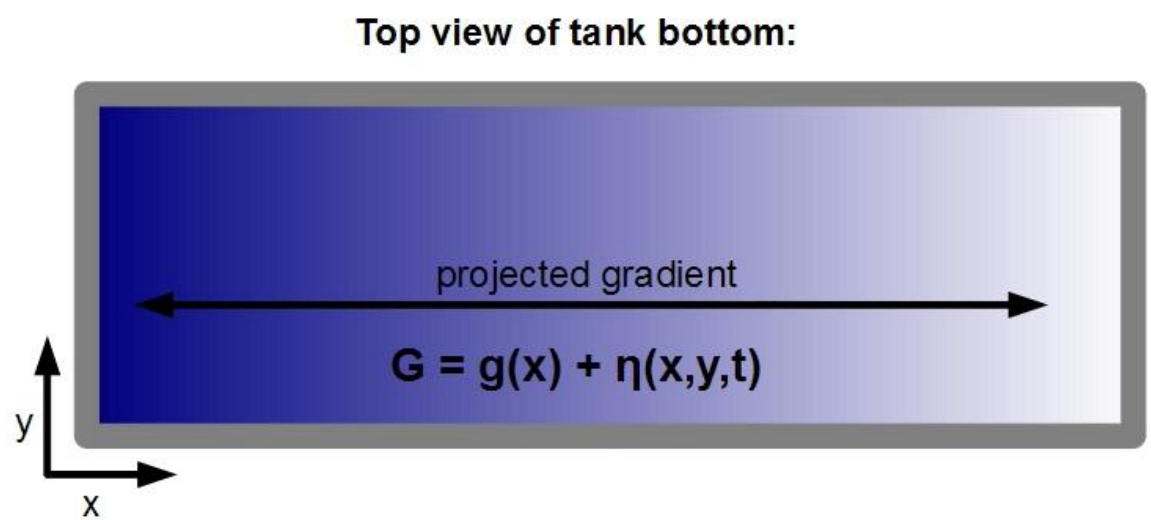


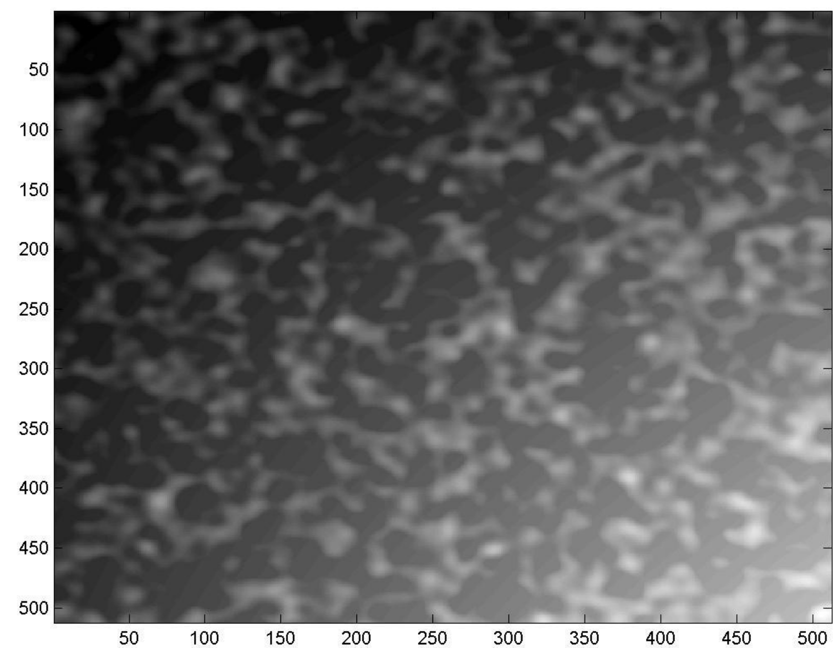
Context-dependent interaction leads to emergent search behavior in social aggregates

Colin Torney[a,b,1], Zoltan Neufeld[a], and Iain D. Couzin[b] PNAS | December 29, 2009 | vol. 106 | no. 52 |

Evolution of migration

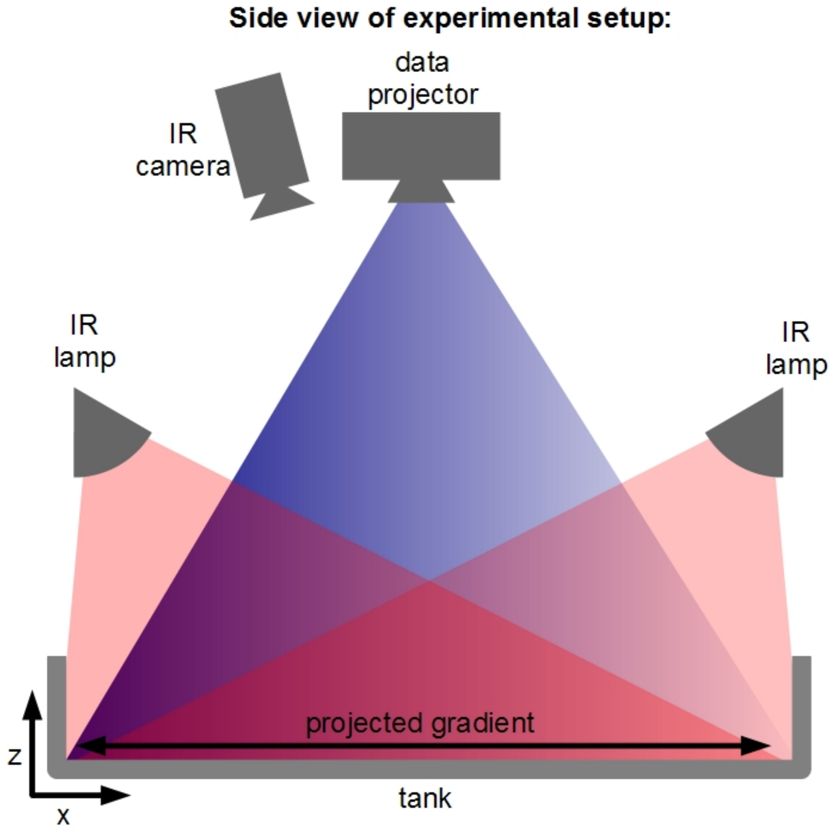
Testing the Theory



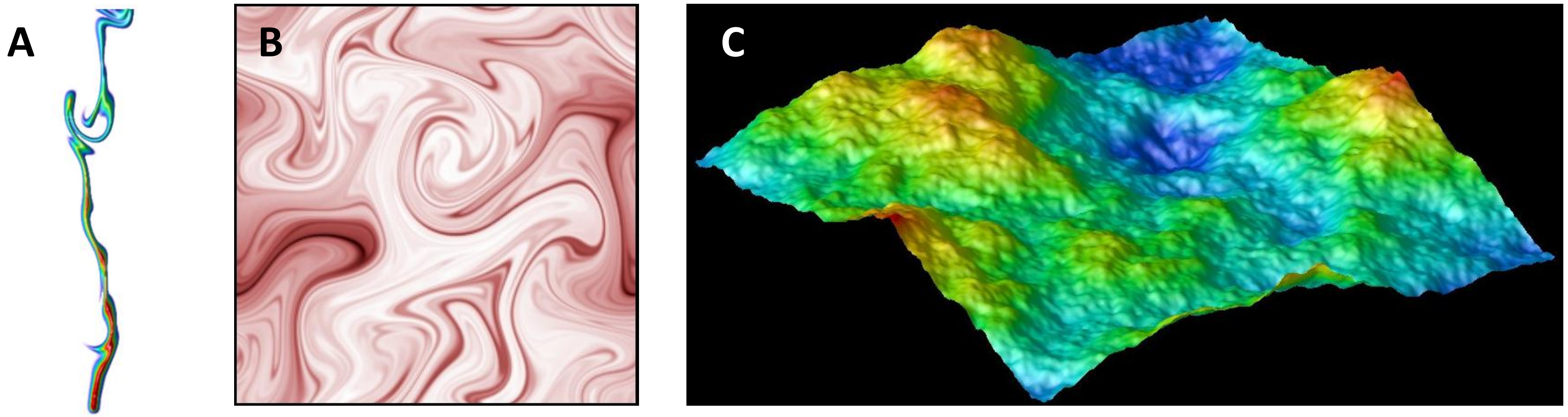


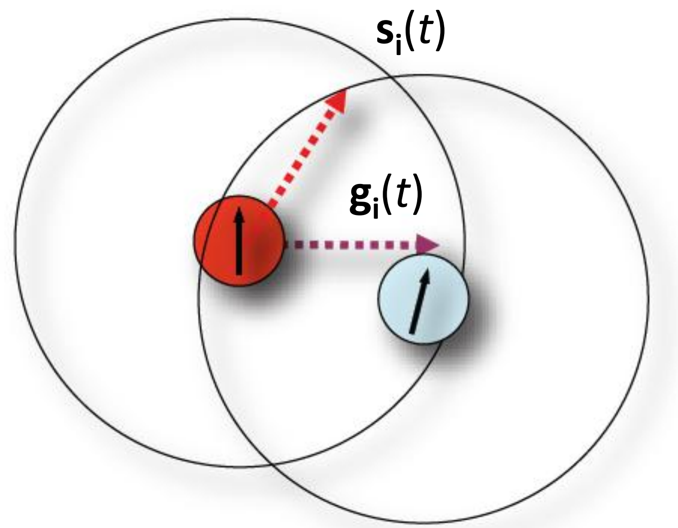
Evolution of migration

Testing the Theory



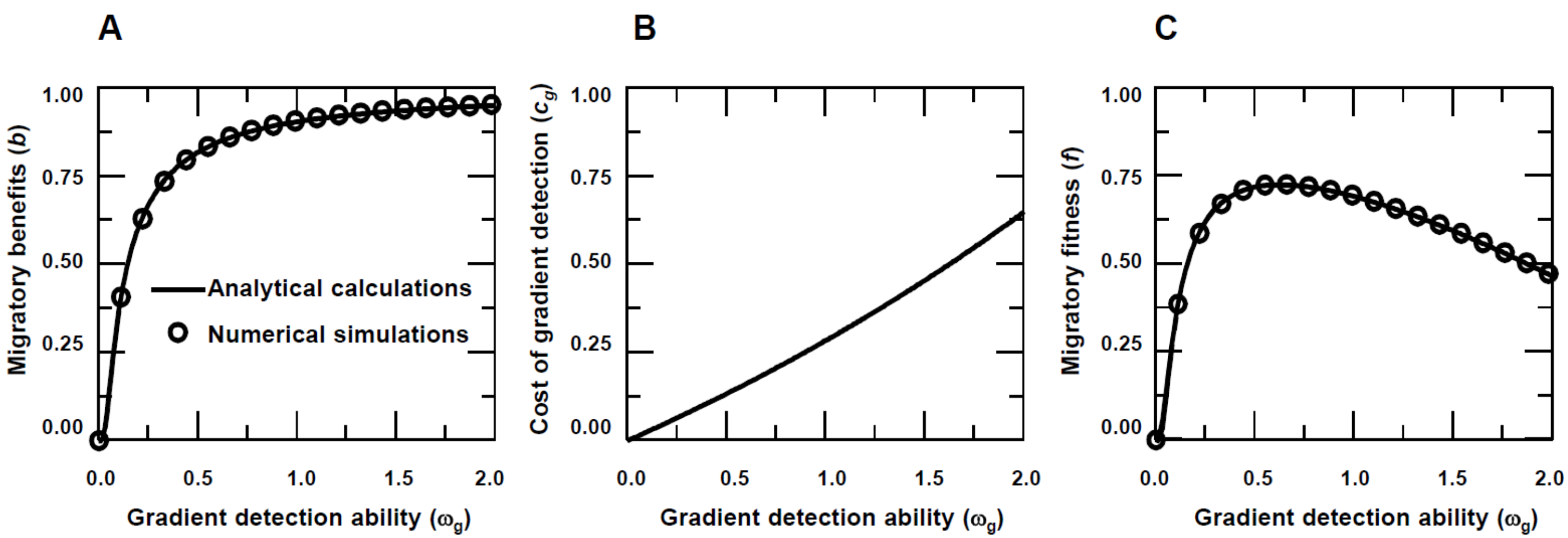
Costs and Benefits of Responding to Noisy Environmental Gradients





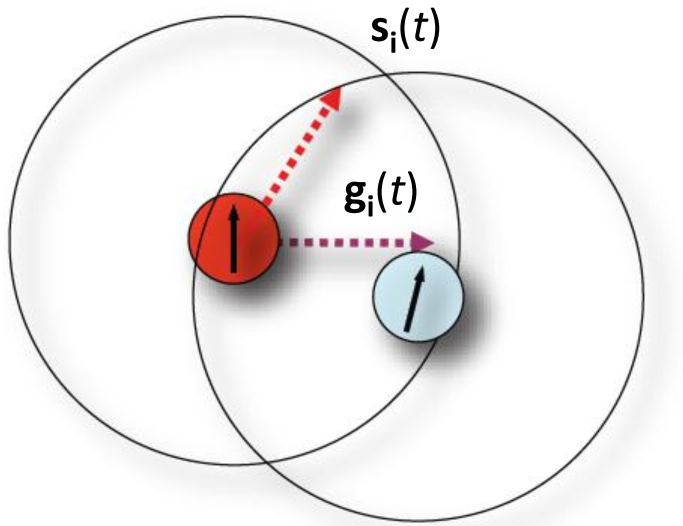
Evolution of migration

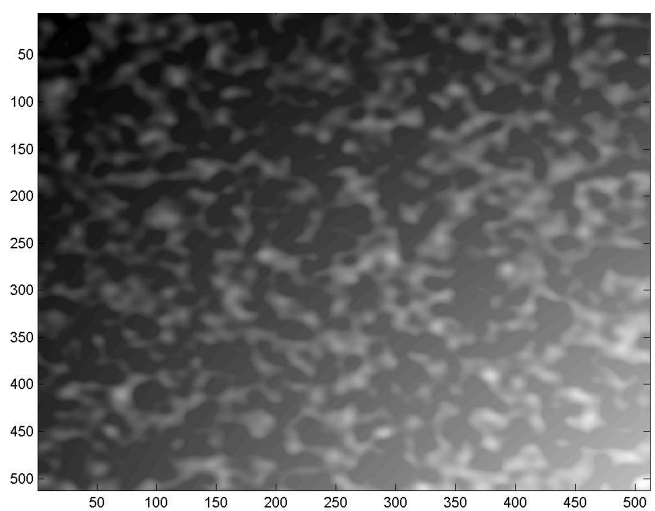
Costs and Benefits of Responding to Noisy Environmental Gradients



But individuals are not cooperative, they are **selfish**

Guttal & Couzin (2010), *in review*





All individuals have 2 evolvable parameters:

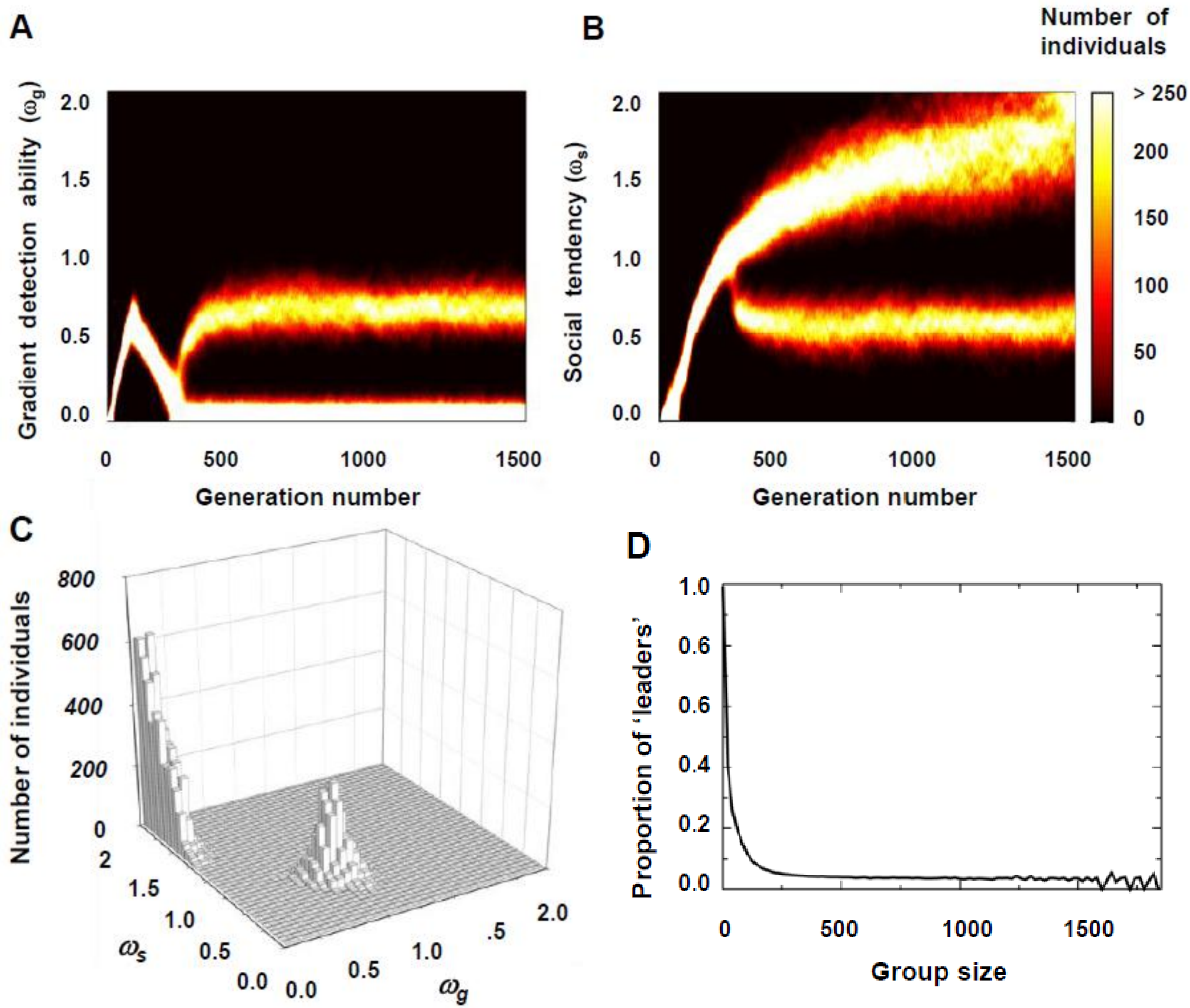
ω_g = gradient detection ability

ω_s = sociality

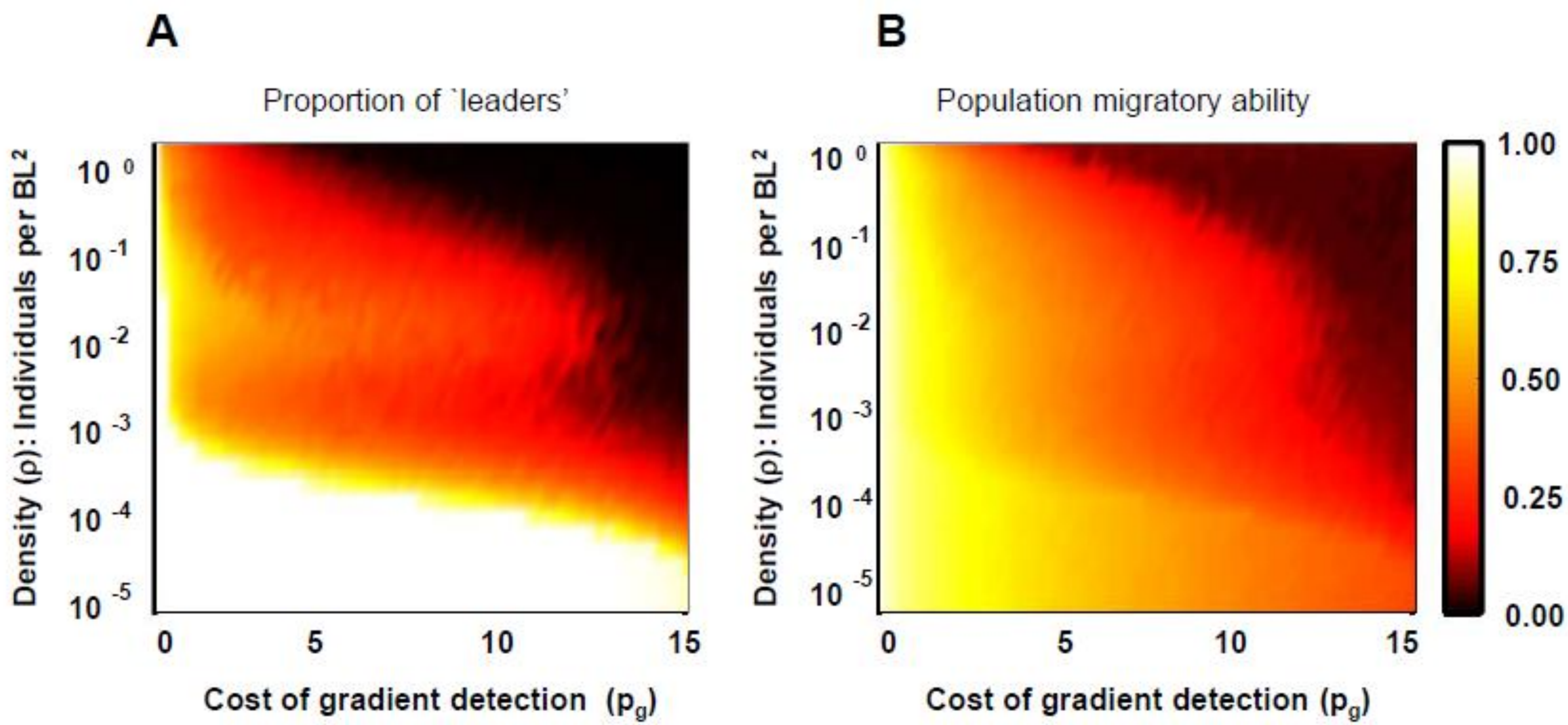
Evolution of migration

Evolution of Collective Migration

Guttal & Couzin, *in review*

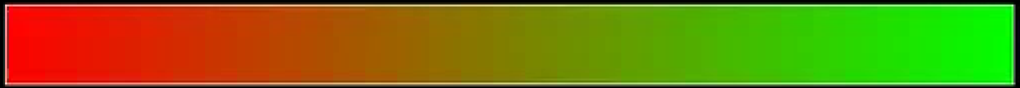


Evolution of migration



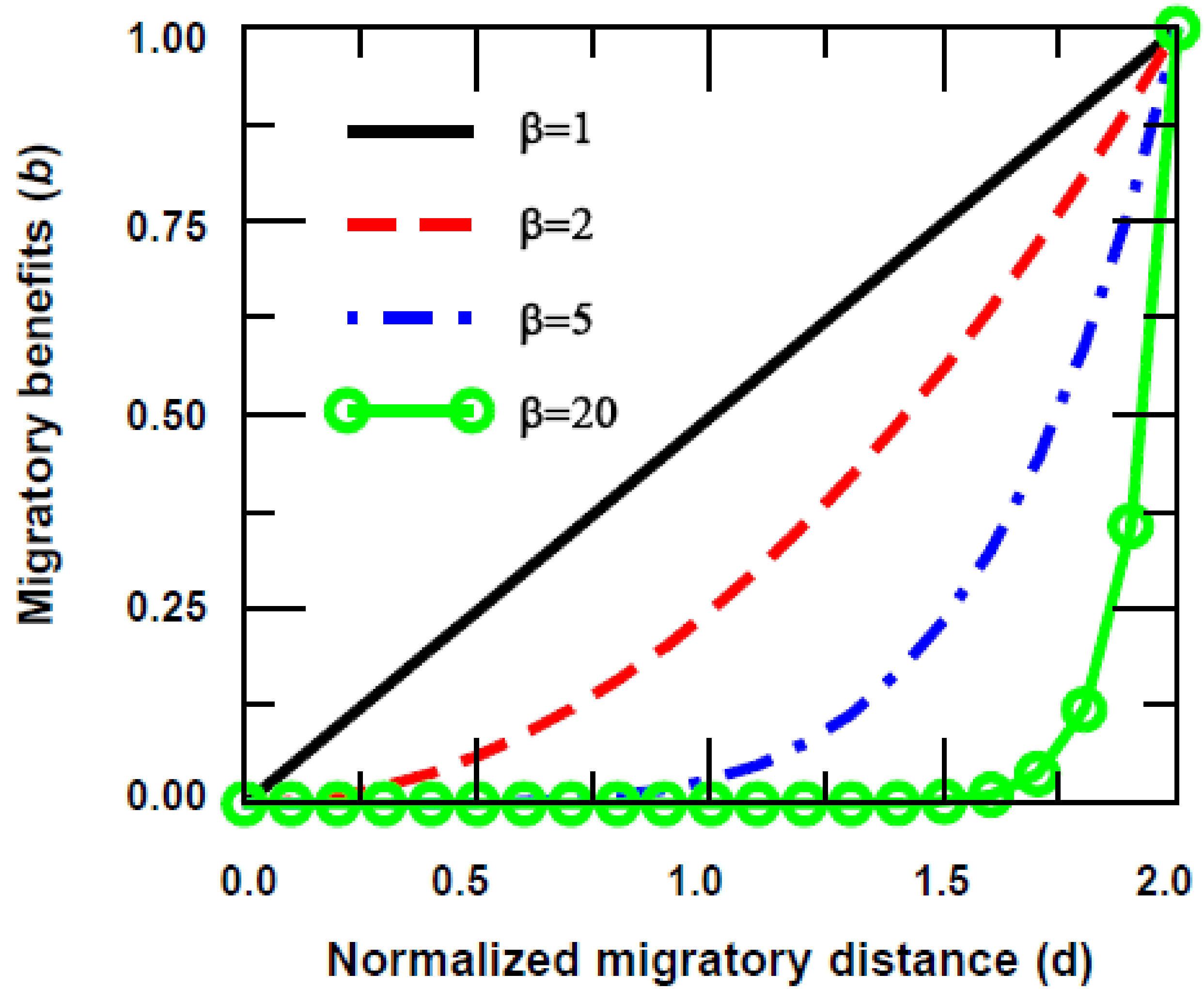
TRANSIENT PHASE

$\omega_G = 0$ $\omega_G = 1$

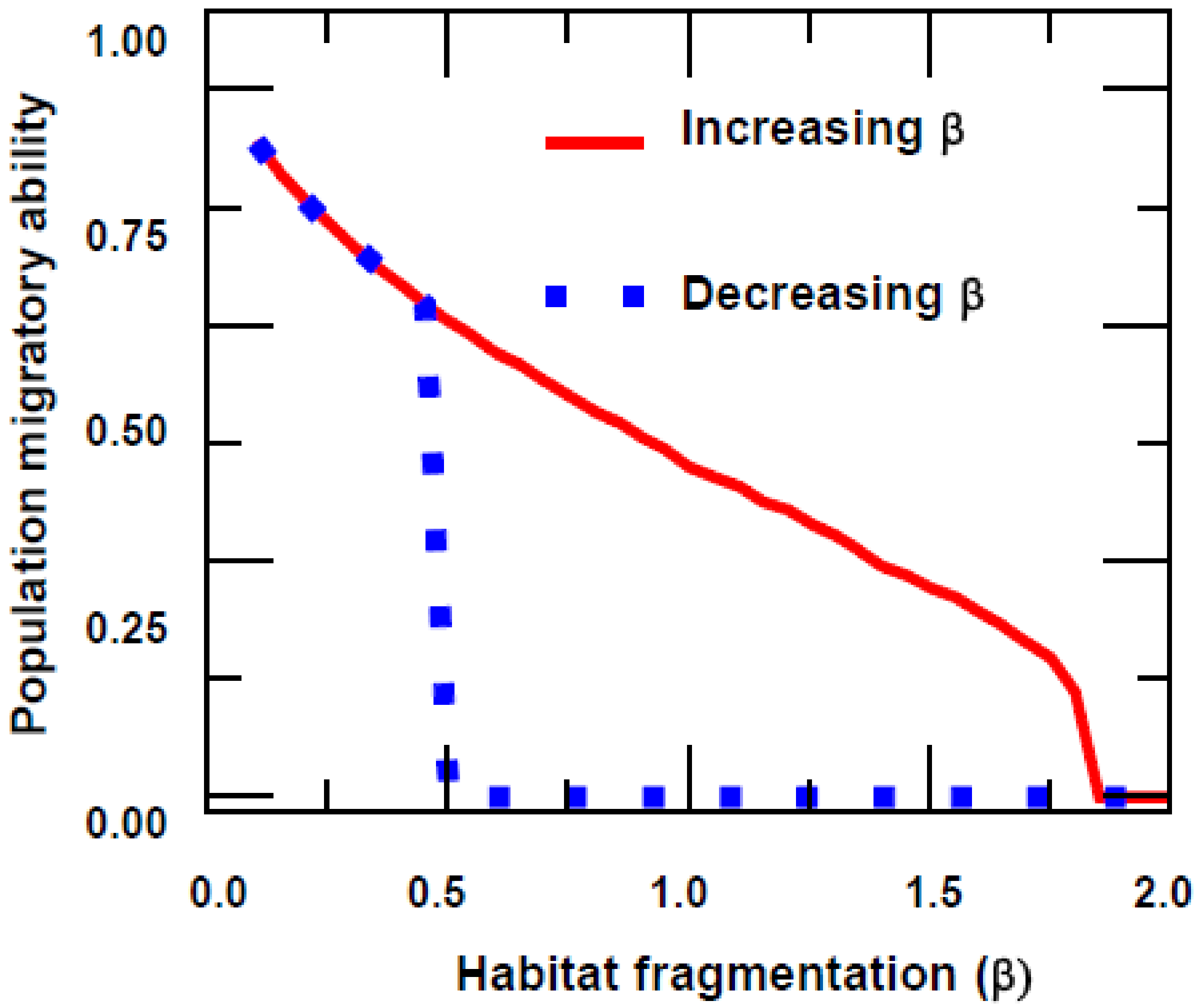


MIGRATORY PHASE

Evolution of migration



Evolution of migration



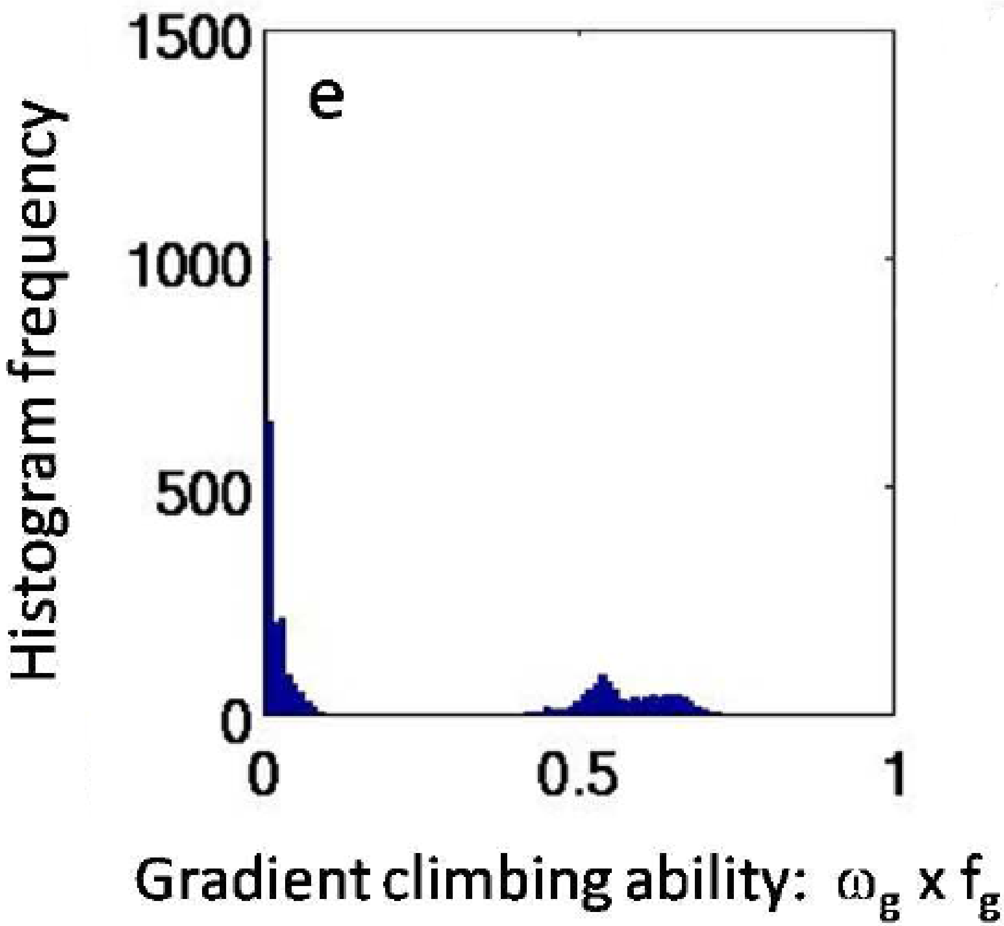
More complex abilities

What if you can switch strategies stochastically?

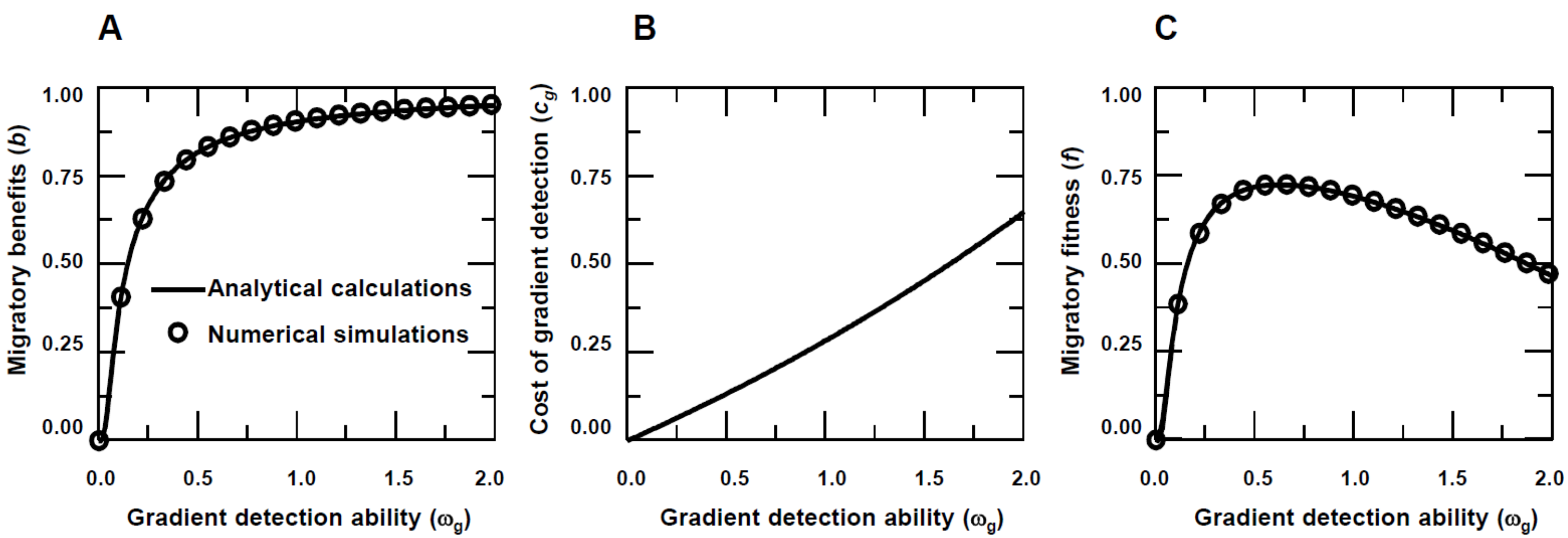
What if you can switch strategies in a context-dependent way?

e.g. in order to avoid being exploited by social individuals, and/or to exploit others with gradient detection ability, an individual may not perform gradient detection when the local environment is crowded (quorum-sensing) despite possessing a high gradient climbing ability (ω_g)

More complex abilities

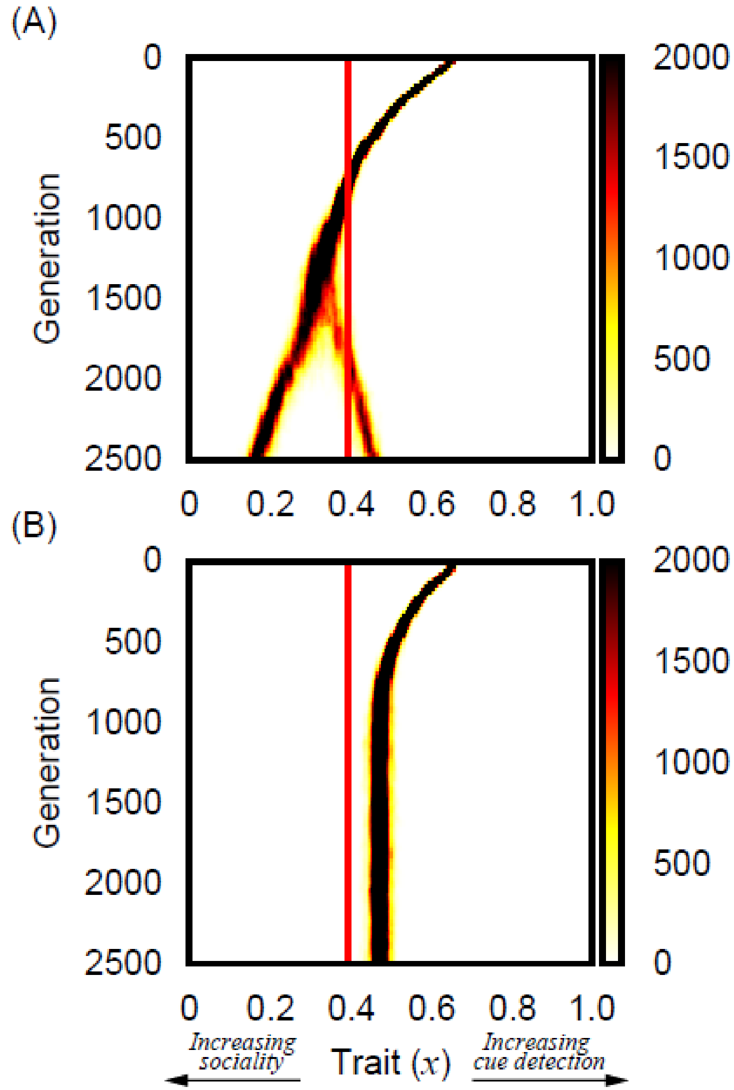


Costs and Benefits of Responding to Noisy Environmental Gradients



But what if groups are of high relatedness (e.g. clonal)

Evolution of migration

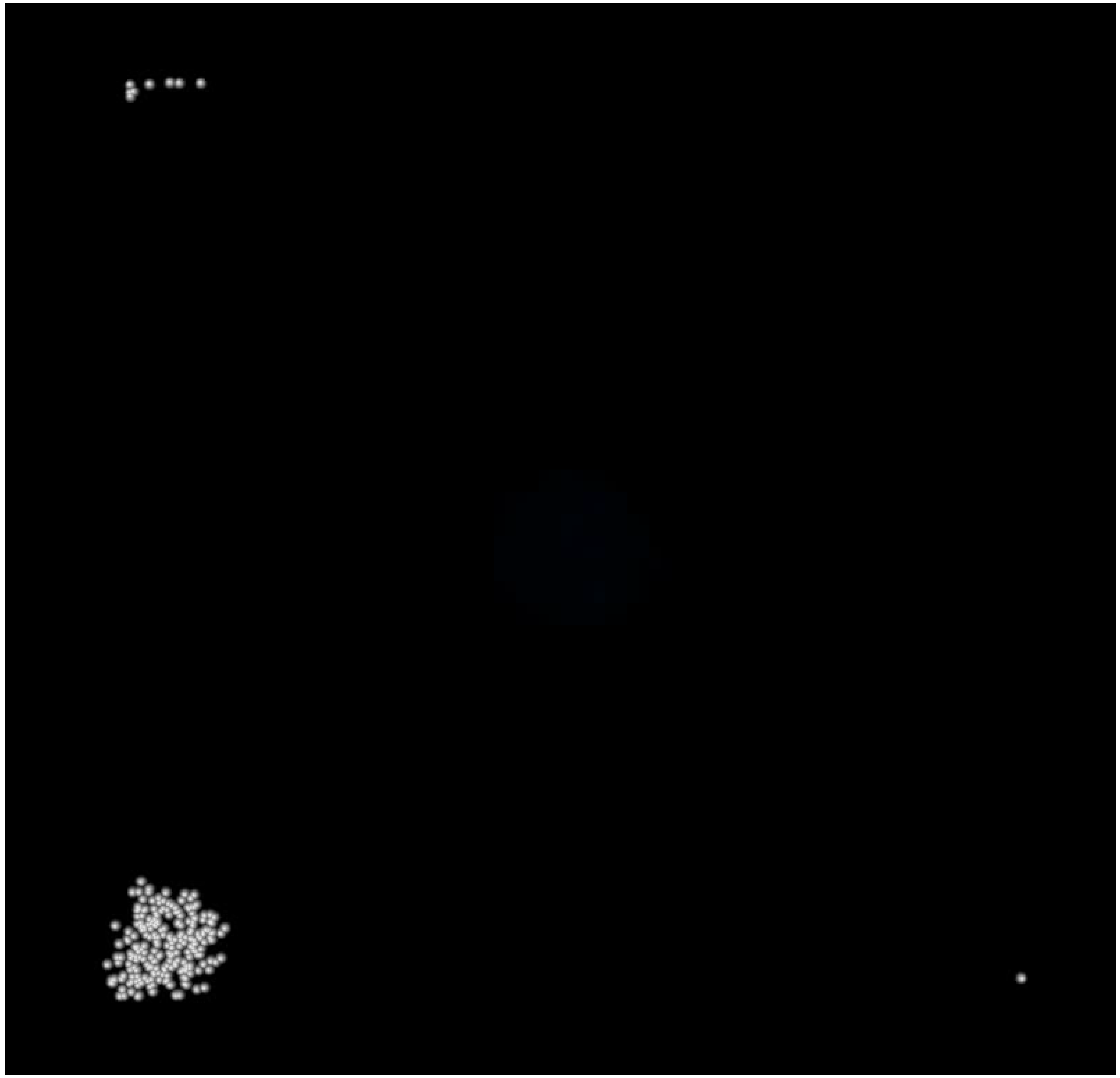


Specialization and evolutionary branching within migratory populations

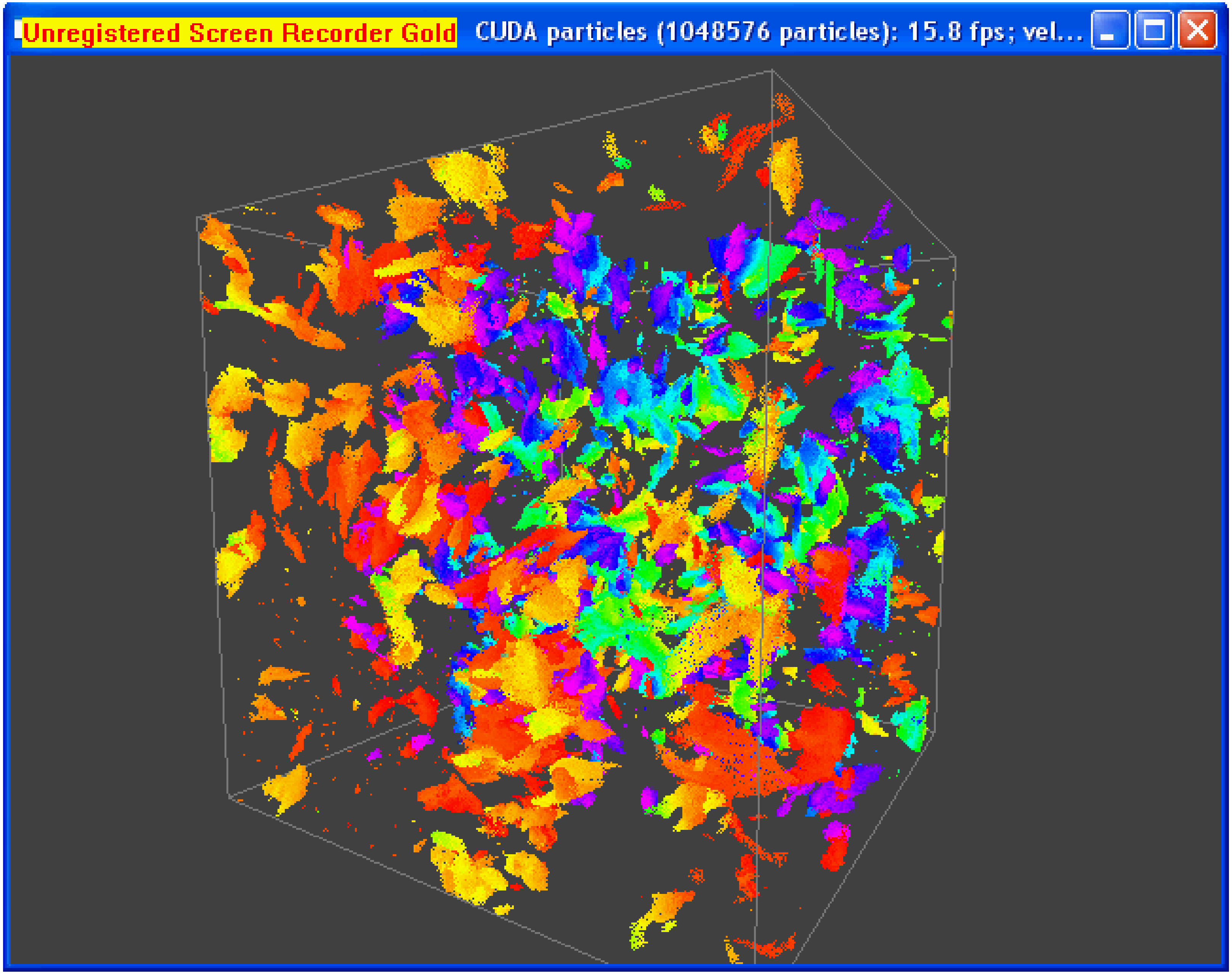
Colin J. Torney *, **Simon A. Levin** * **and Iain D. Couzin** *

*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544

Evolution of migration



Colin Torney


Unregistered Screen Recorder Gold
CUDA particles (1048576 particles): 15.8 fps; vel...

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